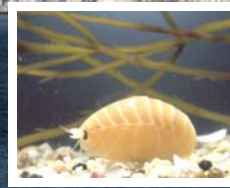


ROLE OF BENTHIC AMPHIPODS IN ANTARCTIC TROPHODYNAMICS: A MULTIDISCIPLINARY STUDY



FABIENNE NYSEN

Dissertation presented in fulfillment for the degree of Doctor of Sciences
2004-2005

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Cette recherche a été réalisée dans le laboratoire d'océanologie de l'Université de Liège ainsi qu'au sein du laboratoire de carcinologie de l'Institut Royal des Sciences naturelles de Belgique à Bruxelles. Cette double appartenance, bien que peu évidente à gérer au début sans pour autant me rendre schizo (à Bruxelles: tiens vlà la Liégeoise! A Liège: tiens vlà la Bruxelloise!...) n'a rendu ce travail que plus riche en expériences de vie et professionnelles, en rencontres intéressantes et surprenantes, bref, en tout! Mais le risque d'oublier l'un ou l'autre se voit doublé...

Tout d'abord, je voudrais remercier le Professeur Jean-Marie Bouqueneau qui m'a accueillie dans son labo au tout début et qui m'a, de ce fait, permis d'accéder aux joies (et aux peines parfois) de la recherche en océanologie.

Ensuite, c'est avec plaisir que je remercie ceux qui sont derrière cette thèse depuis sa genèse, mes promoteur et co-promoteur, le Professeur Patrick Dauby et le Dr Claude DeBroyer.

Claude, merci de m'avoir ouvert les portes de l'Antarctique, ce furent deux expériences magnifiques qui a elles seules peuvent effacer sans peine les moins bons côtés d'une thèse et la sueur qu'elle a fait couler sur mon front, sincèrement merci !!

Quant à Patrick, pour m'avoir supportée (au sens propre comme au sens figuré...) sur terre comme sur mer, pour tes conseils, pour ton humour qui me perdra, pour ton soutien dans les moments moins comiques, pour le café du matin (!!) et pour tout le reste, sincèrement MERCI.

I am pleased to thank the Dr Thomas Brey, for all he gave me during this thesis. First you did contribute by providing me my first Antarctic samples. A bit later, I had the pleasure to meet you on board Polarstern where I have had the privilege to appreciate your bitter sense of humour" and your optimism for all situation (Alles wird sgut!!!!)!!! Maybe my mind will change when I'll be under your "authority" next year to carry our Marie Curie Project but I don't think so... But anyway, THANK YOU!

All my gratitude will go also to the other "German contribution" to this thesis: the Professor Gerard Kattner and more particularly, the Dr. Martin Graeve. Thanks to

have welcome a messy girl like me in your tidy and so efficient laboratory. I learned a lot and did appreciate your kindness and your disponibility. Thanks also to Marco Boer who had “the pleasure” to teach me how to “cook” fatty acids...

To go on with Germany, I'd like to thank those who gave me the opportunities to meet Antarctica: Prof. Wolf Arntz & Prof. Angelika Brandt. Big thank to all the Polarstern “Mannschaft” for his professionalism in resolving all tricky situations and for his kindness.

Numerous places have been a bit as homes for me and I thank here all persons who made me feel as if I was home: my Polarstern roommate in the Blue Cabin: Katja, who also welcomed me at her place every time I had to come to Bremen, I am glad to thank you and your family for the warm atmosphere I had the chance to share. I would like also to say thank you to all the other German and non German mates I had the pleasure to share work and to have fun with, from Chile to Antarctica, through South Africa: Ute, Eva, Kerstin, Felix, Nils, the “Bender team”, Olaf, John, Mike, Louise, Pedro, Mercedes, Julian (thanks for the wonderful pictures), Fani, Enrique, Nuria, Casey and the others, without forgetting Dieter Gerdes and his wife Sabine and Rainer Knust for all they are!!

Après les relations internationales, j'en reviens à ma petite Belgique où j'ai aussi des tas de gens à remercier.

Pour commencer par l'IRSNB, milliards de milliards de mercis à Pollux et Thierry et Isa et Gauthier pour avoir fait de mon travail à Bruxelles, un plaisir !!!! Sans oublier d'ajouter qu'un ami comme toi, Pollo, ça se garde précieusement !! Merci à Henri pour les dépannages ‘supermégaargentissimesdedernièreminute’ dans de nombreux domaines !!! Je remercie aussi tous les membres de l'IRSNB que j'ai eu le plaisir de côtoyer : Frank, Pico, Françoise, Laurence, Yves, Julien (merci pour les photos au scan), Ariane, Veerle et bien d'autres encore.

Poursuivons par le labo d'océano où j'ai fait mes premiers pas dans la recherche.

Tout d'abord, merci à Gilles pour tous ses conseils, son aide précieuse dans les analyses, ses expressions bien à lui, sa patience à toute épreuve et sa gentillesse.

Merci à mes deux expat', ex-collègues préférées : Rachel et Nadège, on a ri ensemble, on a pleuré aussi ensemble mais, à recommencer, je signe des deux mains. Merci pour votre amitié !!

Je remercie Sylvie, Krishna, Denis, Virginie, Laure-So, Baptiste (merci pour ton amitié, ton humour parfois douteux haha et pour les foireux lurons que tu as un peu partagé avec moi, on s'est bien « piché » comme tu dis...), Marc, les étudiants, Martine, Isa et Emmanuelle (pour les agréables et comiques pauses de midi) Renzo, JMT, et les autres membres de la famille océano, pour vos conseils (dans tout domaine !), votre disponibilité et votre agréable compagnie au laboratoire.

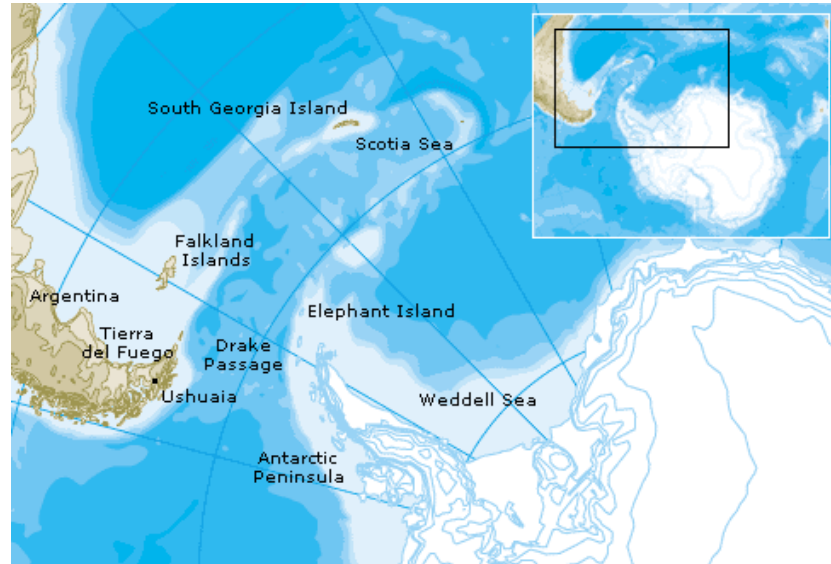
J'en profite car on ne le fait jamais assez dans une vie pour remercier mes parents pour m'avoir permis d'aboutir, mon frère et ma sœur, pour ce qu'ils m'apportent, ma famille pour être ma famille et mes amis pour être restés mes amis ;-)

Finalement je voudrais te dire merci Olivier pour tout ce que tu es pour moi, pour tout ce que tu m'apportes (et tout ce que tu as fait pour alléger ces loooooongues dernières journées ;-)) et pour notre petit J... qui, par son arrivée, malgré les nausées, les kilos en trop et les coups de pied, m'a donné l'énergie nécessaire pour y arriver....

Ce travail a reçu l'appui financier du Fond de la Recherche pour l'Industrie et l'Agriculture (FRIA) et des Services Fédéraux pour les affaires Scientifiques Techniques et Culturelles (SSTC, Programme antarctique, phases IV et V)

OBJECTIVES

The purpose of this work is to assess the ecological roles of amphipod crustaceans in the Southern Ocean and, more particularly, on the continental shelf of the Weddell Sea and the Antarctic Peninsula.



Within this ecological study, focus has been made on the significance of amphipods in Antarctic trophodynamics through:

- A systematic determination of gut content composition. The amphipods have been chosen because they cover an extremely wide trophic spectrum; from sampling gathering suspension-feeders such as *Ampelisca richardsoni* to micropredators such as *Epimeria similis*, as well as scavengers such as *Waldeckia obesa*. The species considered in this work are representative of the Antarctic continental shelf amphipod community.

- An scan examination of the morphology of the mouthparts and especially of the mandibles in several species, representative of different trophic types.
- A systematic analysis of stable isotope ratios $-\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ - in all the sampled species in order to estimate and compare their respective trophic position. The isotopic ratios have also been measured in specimens of other benthic groups to investigate the trophic relationships built by amphipods in the Antarctic benthic food web.
- The determination of the fatty acid composition in several species of amphipods to delineate the trophic links between amphipods and the rest of benthos.

This multidisciplinary approach allows tackling the complex problem of amphipod trophic role in the Southern Ocean from different angles, each adding a particular aspect to overall food web picture.

The general introduction and results are presented according to the following framework:

Chapter 1: A general introduction puts the scientific question in its global context by summarizing information about the studied ecosystem: the Southern Ocean and the significance of amphipods in Antarctic benthic communities. The second part of this introduction is devoted to the description of the different techniques that have been used to assess benthic amphipod ecological role in Antarctic trophodynamics.

Some of the following chapters have already been published in peer-review journals or submitted.

Chapter 2: “*A stable isotope approach to the Eastern Weddell Sea trophic web: focus on benthic amphipods*”, Polar Biology (2002) 25: 280-287.

Chapter 3: “*Trophic position of Antarctic amphipods - enhanced analysis by a 2-dimensional biomarker assay*”, Marine Ecology Progress Series, (2005) in press.

Chapter 4: “*Antarctic amphipod feeding habits inferred from gut contents and mandible morphology*”, to be submitted.

Chapter 5: “*The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities*” Deep-Sea Research, part II (2004) 51: 1733-1752.

Chapter 6: “*Amphipods as food sources for higher trophic levels in the Southern Ocean: a synthesis*”, In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys Publ, Leiden, (2003) p 129-134.

Chapter 7: *General Discussion and Conclusions.*

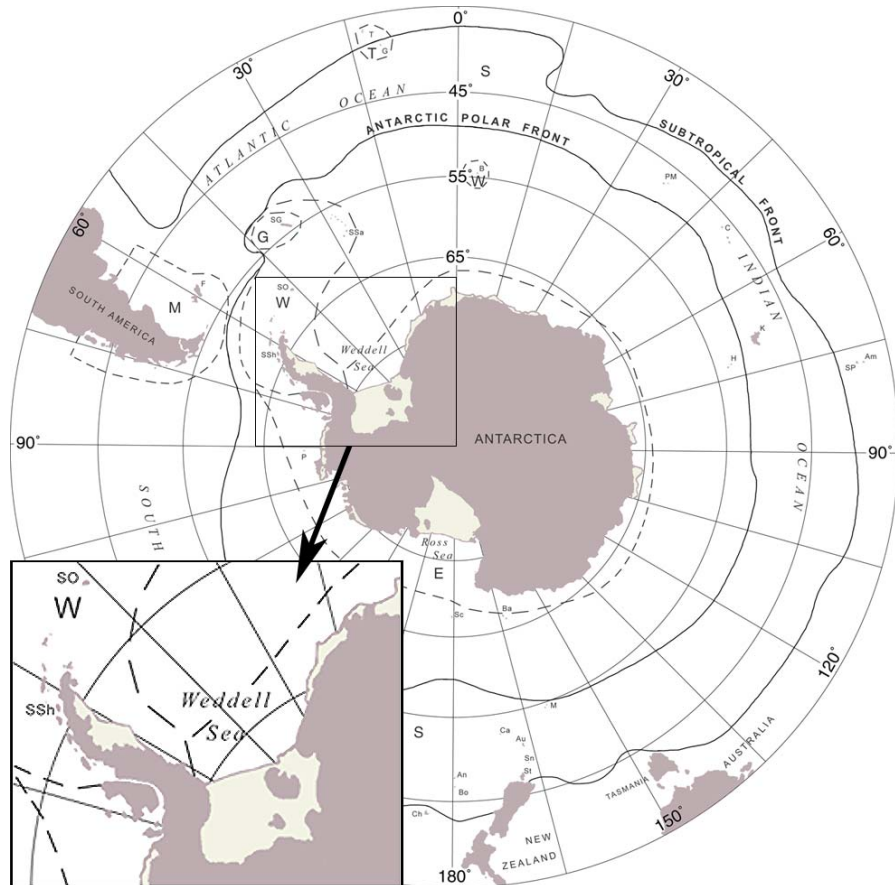
CHAPTER 1: GENERAL INTRODUCTION

1.1. THE SOUTHERN OCEAN

1.1.1. OCEANOGRAPHIC FEATURES

The Southern Ocean consists of the southern parts of the Atlantic, Indian and Pacific oceans (Fig 1.1.). Used in its wide sense, according to Deacon (1984), the Southern Ocean includes all waters south of the Subtropical Front zone (at about 42°S). In its restricted sense, it comprises only the waters extended south of the Polar Front (50°S in the Atlantic and Indian sectors and 60°S in the Pacific sector) (e.g. Dell 1972, Clarke 1996a). We will privilege the restricted sense of the definition. The northern boundary of the Southern Ocean, the Antarctic Polar Front, is characterized by a steep surface temperature gradient of 3–4°C, as well as by changes in other oceanographic parameters like salinity. At the frontal boundary, northward-flowing Antarctic Surface Water sinks beneath warmer Subantarctic Surface Water, generating a transition zone between surface water masses of different temperatures. From an oceanographic perspective, the surface circulation around Antarctica consists of two main currents. Close to the Antarctic Continent, easterly winds generate a counterclockwise water circulation, i.e. the Antarctic Coastal Current or East Wind Drift. North of 60°S, westerly winds produce a clockwise and northward water flow, known as Antarctic Circumpolar Current or West Wind Drift, representing the major current in the Southern Ocean. In large embayments of the Antarctic Continent, particularly the Weddell and Ross Seas, the Antarctic Coastal Current forms clockwise gyres, which probably concentrate nutrients like silicate, phosphate and nitrate. Unlike other areas of Antarctica, the continental shelves of the Weddell and Ross Seas are wide and 500–600 m deep, with inner shelf depressions reaching depths of over 1,200 m (Anderson 1999). Furthermore, much of the Antarctic coastline is covered by ice shelves, which are exceptionally large in the Weddell and Ross Seas. During much of the year, the adjacent shelf waters are covered by pack ice.

Figure 1.1. Map of Southern Ocean and detail displaying sampling zones: the Weddell Sea and the Antarctic Peninsula. SO: South Orkney Islands, SSh: South Shetland Islands, F: Falklands, E: East Antarctic sub-region, W: West Antarctic sub-region (including South Georgia district), S: Subantarctic sub-region, M: Magellanic sub-region, T: Tristan da Cunha district



The most obvious physico-chemical characteristic of the Antarctic coastal and shelf ecosystem (ACSE) is the year round low water temperature. For example, temperature close to the sea bed varies annually between 0 and 3°C in South Georgia (54° S), -1.8 and 2°C in the South Orkney Islands (West Antarctic, 61° S), and -1.9 and -1.8°C at McMurdo Sound (East Antarctic, 78° S) (Clarke 1983). This low and – compared to boreal waters - very stable temperature has important biological consequences. For instance, the inverse relationship between gas solubility and temperature leads to extraordinary high levels of oxygen in Antarctic waters. Another major characteristic of the ACSE is the highly seasonal character of the primary production (Clarke 1988). This primary production relies mainly on phytoplankton, not only in the shelf waters, but also in the intertidal and shallow subtidal areas, due to the paucity of macroalgae resulting from the negative impact of ice bergs, brash ice and solid ice on the macroalgae (Clarke 1996a). Compared to warmer latitudes, this primary bloom is also more decoupled from the grazing bloom of the zooplankton, ensuring an important phytoplankton input to the sea floor (Gray 2001).

The seasonally ice-covered regions of the Southern Ocean feature distinct ecological systems due to sea ice microalgae . Although sea ice microalgal production is exceeded by phytoplankton production on an annual basis in most offshore regions of the Southern Ocean, blooms of sea ice algae differ considerably from the phytoplankton in terms of timing and distribution. Thus sea ice algae provide food resources for higher trophic level organisms in seasons and regions where water column biological production is low or negligible. A flux of biogenic material from sea ice to the water column and benthos follows ice melt, and some of the algal species are known to occur in ensuing phytoplankton blooms. A review of algal species in pack ice and offshore plankton showed that three species are commonly dominant: *Phaeocystis antarctica*, *Fragilariopsis cylindrus* and *Fragilariopsis curta* (Lizotte 2001). As pointed out by Grassle (1989), spatial patchiness of

organic matter sedimentation is highest in Polar Regions, and this could in part account for the high diversity of the Antarctic benthos, together with the - still controversially discussed - link between energy input and diversity (Gage & Tyler, 1991; Roy et al., 1998; Gray, 2001).

Also important is the physical disturbance caused by icebergs. This adds to the heterogeneity of the environment and increases niche diversity (Arntz et al. 1997). According to a recent assessment, iceberg scouring is one of the 5 most significant physical impacts on any ecosystem on Earth (Garwood et al. 1979, Gutt & Starman 2001). It has most likely been a major driving force in structuring Antarctic benthos since the continent began to cool and glaciers extended up to the coast approx 25 to 30 million yr ago (Hambrey et al. 1991). Mainly quantitative effects of scouring on meio- and macrobenthos have been described and reviewed by Gutt et al. (1996), Conlan et al. (1998), Peck et al. (1999), Gutt (2001) and Lee et al. (2001a, b). Type and strength of physical iceberg impact on the benthos vary (e.g. Kauffmann 1974), but it is estimated that 5% of the Antarctic shelf shows detectable scours (Gutt et al. 1999). Iceberg impact causes various degree of damage to the benthos up to local extinction of the fauna (Dayton et al. 1974, Brey & Clarke 1993, Arntz et al. 1994, Peck et al. 1999) and disturbed bottoms are subsequently recolonized. Temporal distribution of iceberg scouring and time-scale of recolonization are still poorly understood, but seem to be an intrinsic feature of Antarctic shallow-water and shelf benthic community dynamics leading to a spatial and temporal patchwork of benthic recovery (Gutt et al. 1999, Brenner et al. 2001, Texeido et al. 2004).

Another factor responsible for this higher diversity compared to the Arctic is the long evolutionary history of the Southern Ocean (Clarke, 1996b). When the first has only been isolated 2-3 million years ago, separation of the Antarctic occurred at least 25 million years ago (Dunton, 1992; Dayton et al., 1994; Clarke & Crame, 1997).

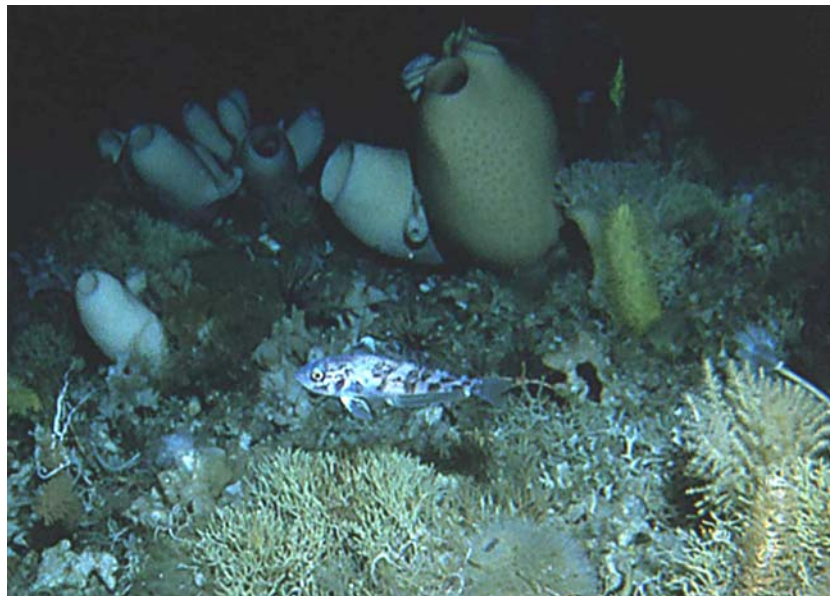
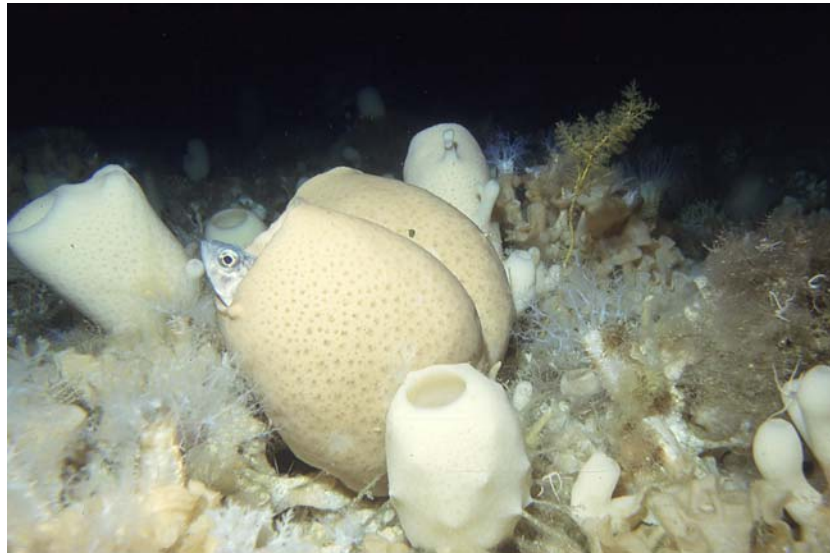
1.1.2. BENTHOS BIODIVERSITY IN THE SOUTHERN OCEAN

1.1.2.1. The Antarctic benthos

Antarctic marine biodiversity is strongly influenced by the geological and glaciological history of the Antarctic continent. The origin of distinct benthic marine invertebrate faunas in both Antarctic and Subantarctic waters can be traced back as far as the Early Cretaceous, about 130 million years ago, when the break-up of the Gondwana continent first became evident, and eastern Gondwana became isolated in the high southern latitudes (Lawver et al. 1992; Crame 1999). Antarctic cooling may have started as late as 35 million years ago as a result of ongoing continental drift and the establishment of the Antarctic Circum-polar Current (Barker et al. 1991), leading to an isolation of the Antarctic marine realm from surrounding seas (Clarke 1990).

Recent observations, notably by video underwater cameras coupled with analyses of benthos samples, have described a variety of benthic assemblages from the eastern Weddell Sea shelf (i.e. Galéron et al. 1992, Gutt & Schickan 1998). As our study had focused particularly on this part of Southern Ocean and because of the numerous studies already conducted on Weddell Sea benthic communities, we will take it as our reference in terms for Antarctic benthos. The unusually deep continental shelf of the Weddell Sea locally exhibits a complex 3-dimensional community with patchy distribution of organisms (Gutt & Starmans 1998, Gili et al. 2001, Teixidó et al. 2002, Gerdes et al. 2003). The fauna in this area is dominated by a large proportion of benthic suspension feeders such as sponges, gorgonians, bryozoans and ascidians, which locally cover most of the sediment (Gutt & Starmans 1998, Starmans et al. 1999, Teixidó et al. 2002). Those diverse and multistratified sessile benthic assemblages offer a high diversity of potential microhabitats to small vagile invertebrates (see Fig. 1.2 & 1.3).

Figures 1.2 & 1.3. Illustrations of typical Antarctic sessile benthic assemblages composed of sponges, bryozoans, cnidarians... (Photos from Julian Gutt, AWI)



In a recent overview of Antarctic marine biodiversity, Arntz et al. (1997) compiled the species numbers per taxon for most groups of marine animals and plants occurring south of the Polar Front. This compilation, albeit yet being far from representing the complete Antarctic species inventory, clearly shows the relative importance of polychaetes and mollusks and the predominance of crustaceans. In terms of composition, more particularly, the Antarctic crustacean fauna includes some extreme groups, from a total absence for some taxa to particular richness for others:

- **Stomatopoda.** They are totally lacking in Polar seas.
- **Cirripedia.** They are characterized by the extremely high proportion of lepadiform versus balaniform. This seems to be correlated with the lack of suitable littoral habitats and with the geological history of Antarctica (Dell 1972).
- **Decapoda.** The impoverished Antarctic decapod fauna, compared with the high diversity of decapod crustaceans recorded in the Subantarctic (Gorny 1999), constitutes one of the most enigmatic phenomena in present-day marine biodiversity research. The decapod fauna composition was reviewed by Gorny (1999). Twenty-four decapods (12 pelagic and 12 benthic species) occur south of the Antarctic Convergence. They represent only 0.25% of the world decapod fauna. Different hypotheses were proposed to explain the poor decapod fauna and the absence of the whole group of brachyurans. Low temperatures in general have been hypothesised to reduce decapod activity, especially in combination with high $[Mg^{2+}]$ levels in the haemolymph, as $[Mg^{2+}]$ has a relaxant effect (Frederich 1999; Frederich et al. 2001). Since Reptantia regulate $[Mg^{2+}]_{HL}$ only slightly below the $[Mg^{2+}]$ of seawater, their activity should be hampered. In contrast, Natantia are known to regulate $[Mg^{2+}]_{HL}$ to very low levels (Tentori and Lockwood 1990; Frederich et al. 2001). The combined effect of low temperatures and high $[Mg^{2+}]_{HL}$ might explain the limits of cold tolerance in decapods and might be the principal

reason for the absence of reptant decapods from the high polar regions (Frederich et al. 2001). At present only lithodids may tolerate environmental and physiological constraints imposed by the low temperatures and short periods of food availability at high- Antarctic latitudes (Clarke 1983, Thatje 2003a, Thatje and Fuentes 2003b, Thatje et al. 2003c, Thatje et al. 2004). On the other hand, among the Antarctic crustacean fauna, amphipods and isopods form obviously highly species-rich groups. This will be described in details in the section 1.2. The issue of the Antarctic benthos species richness in a worldwide latitudinal context has been recently discussed in details (Clarke 1992, Clarke & Crame 1997, Crame (1999) and Gray 2001a) but useable data are still too few and of limited comparability. The reasons for latitudinal variation in marine species richness are contentious but most likely related to variation in time available to species diversification and to variation in the area and productivity.

Another interesting aspect of the latitudinal gradient issue is the size distribution within marine organisms. Significant progress has been made recently in elucidating the trend towards gigantism in polar Crustacea, in particular among the highly species-rich and widely distributed Amphipoda. Indeed, from a large data set, Chapelle & Peck (1999) and Chapelle (2001) confirmed the existence of a clear trend towards larger amphipod species in polar regions and especially in the Antarctic. A crucial finding was that this trend toward larger size is explained best by oxygen content rather than by temperature, with the largest species to be found in waters with the highest oxygen concentration. Chapelle & Peck (1999) and Peck & Chapelle (1999) demonstrated that the maximal potential size in amphipod crustaceans was dictated by oxygen availability.

Circumpolarity in species distribution and extended range of eurybathy were considered as common features in Antarctic benthos (Brey et al 1996). However recent studies have revisited this concept and the most striking progress in this context has been accomplished by molecular methods. For

example, after analyzing the sequences from the mitochondrial 16S ribosomal RNA of the isopod *Ceratoserolis trilobitoides* (Eights, 1833), Held (2003) demonstrated that this species, known as a cosmopolitan and highly plastic species in the Southern Ocean, contains “at least one, possibly many more, previously overlooked species” with poorly overlapping distribution. Furthermore, from a phylogenetic analysis of the circumpolar giant isopod *Glyptonotus antarcticus* Eights, 1853 he concluded that there was good evidence that four different *Glyptonotus* species might exist where only one circumpolar species was recognized so far (DeBroyer et al. 2003).

Another feature of Antarctic zoobenthos is the high degree of species endemism that has been recorded in many taxa (White 1984). Regarding benthic amphipods, 85% of all species are endemic to the Antarctic (DeBroyer & Jazdzewski 1993, 1996).

1.2. AMPHIPODA

1.2.1. WHAT IS AN AMPHIPOD?

1.2.1.1. Systematics

Up to now, Peracarida are still treated as a superorder that contains nine orders in the crustacean classification. However, there have been suggestions made to abandon the Peracarida or at least significantly revise it (e.g. Dahl 1983a), and the relationships among the various peracarid groups (and of peracarids to other groups of crustaceans) are very controversial.

Following the updated classification of crustaceans from Martin & Davis (2001), Peracarida contain the orders Lophogastrida and Mysida, plus the Thermosbaenacea, in addition to the Spelaeogriphacea, Mictacea, Amphipoda, Isopoda, Tanaidacea, and Cumacea.

The most diversified orders are the isopods, with 4,000 species (Brusca & Brusca, 1990), and the **amphipods**, with around 8,000 described species, to which this work is devoted.

Classically, Amphipoda are divided in four suborders; the mainly benthic Gammaridea, the interstitial Ingolfiellidea, the rod-shaped and benthic Caprellidea and the exclusively marine and planktonic Hyperidea. However, Dahl (1977) and later Bowman & Abele (1982) considered that there were only three suborders, by including the Ingolfiellidae within the Gammaridea. This new classification did not last long, as in 1983, Barnard (in Barnard and Karaman, 1983) proposed that the Amphipoda should be divided into three suborders: Corophiidea, Hyperiidea, and Gammaridea. According to their phylogenetic hypothesis, the Ingolfiellidea are placed under Gammaridea, and the Caprellidea are reduced to a superfamily under the new suborder Corophiidea. In this study, we refer to Barnard classification.

With more than 6,000 species, the Gammaridea are by far the most species-rich of these groups. Our study will focus mainly on benthic gammarid species living on the continental shelf.

1.2.1.2. Morphology

Much morphological variation exists within the order Amphipoda. Furthermore, within the suborder Gammaridea, which represents 80% of the species, the shape varies with family. However, all species, as much differentiated as they may be, correspond, at least by a certain amount of characters, to the typical “amphipod common type”. A typical amphipod can be described as a small crustacean, of around 10 mm, with an arched and laterally compressed body divided in three parts (Fig. 1.4.): the head, the 7-segmented pereon and the 6-segmented pleon (Bellan-Santini, 1999).

- The head: the term, commonly used in amphipod taxonomy, is wrong as this part of the body corresponds to a cephalothorax (Bellan-Santini 1999). The head bears sessile eyes, two pairs of antennae and mouthparts.

Eyes are composed of a large amount of ommatidies. Their development is variable: absent in some cave species, the eyes reach a considerable size in some hyperiid species.

The peduncle of the first pair of antennae is smaller than the second, three articles instead of five, respectively. Both are terminated by pluri-articulated flagella.

Most of amphipods mouthparts correspond to a common scheme although a large panel of modifications to the basic pattern can be observed (Watling 1993). Consequently, mouthpart morphology is essential in amphipod taxonomy. The most frequent type bears above and beneath the mouth: an upper lip (*labrum*) and a lower lip (*labium*). Between the lips, around the mouth, the mandibles are found; constituted of an incisor process, generally provided with cusps and teeth; the *lacinia mobilis*, inserted close to the

incisor and generally in line with; the molar process, a plane surface provided with diverse triturative structures and a palp, generally tri-articulated (Watling 1993). Posterior of the lower lip the maxillae 1 followed by the maxillae 2 are found. The following appendages are the maxillipeds.

- The pereon: this part is composed of seven segments, generally well separated but which can be partially fused in some hyperiids. The seven pairs of pereopods borne by the pereon are oriented in two directions: three point towards the rear and four are directed towards the front. This feature is the origin of the name "Amphi - poda".

The pereopods are generally long and brittle, but most frequently the first two pairs are modified in kind of hooks and are so called, gnathopods. A typical pereopod is classically divided - from the proximal to the distal part - in the following parts: coxa, basis, ischium, merus, carpus, propodus and dactylus. The coxa is often flattened in a coxal plate. The Gammaridea present various forms of coxal plate. For example, in the Lysianassidae, the first four coxal plates are highly developed and form a kind of lateral shield and in some Iphimediidae, the coxal plates present characteristic incurvate teeth. The two pairs of gnathopods present different evolutive stages but the most common is the one modified in a claw constituted by a hook-shaped dactylus and a large propodus.

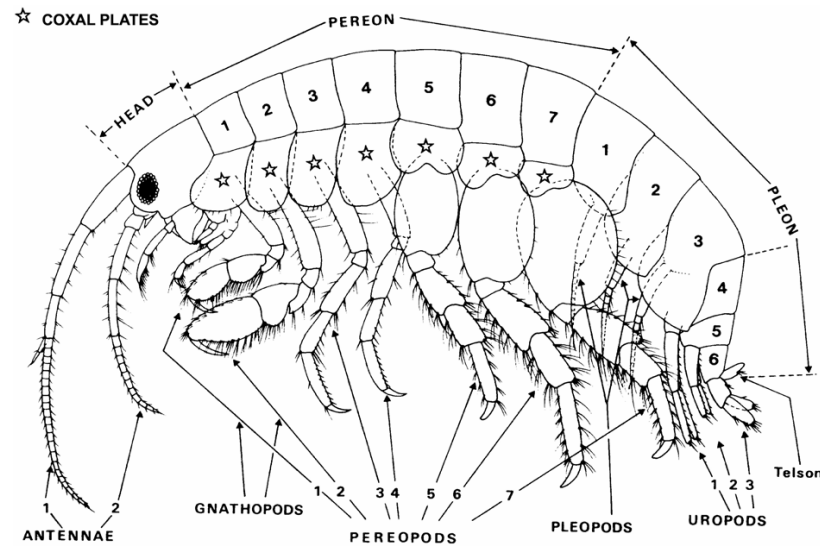
The pereopods bear generally a gill inserted at the junction with the body. Those gills are present from the second to the seventh pereopods but the number can vary.

The oostegites are generally large inner medially directed lamella provided with setae arising from coxa of pereopod in females participating in formation of mid-ventral brood pouch proper to peracarids, "the marsupium".

- The pleon: this part is composed of six somites: the first three (metasome) bear swimming appendages, the pleopods, and the last three bear the uropods (urosome). The pleon is ended by the telson, a kind of blade situated on the last segment of the urosome. It can show various shape following the family

(complete or cut, armed with spines and setae) but can also be strongly reduced. Morphology of telson is a significant taxonomical character.

Fig. 1.4. – Basic morphology of gammaridean amphipod. From Chapelle (2001)



1.2.1.3. Ecology in brief

The Amphipoda inhabit nearly all aquatic habitats. They have been recorded in the hot vents of the deep sea or beneath the polar sea ice, in mountain streams or in caves, in the interstitial water of aquifers or on the bottom of the deepest abyssal trenches, on the skin of cetaceans or inside jellyfish, in the shell of hermit crabs or on the shell of sea turtles, under decaying algae on every beach or in the litter of some rain forests. This habitat diversity is coupled to an equally diverse trophic spectrum; amphipods comprise specialized predators, herbivores, scavengers, detritivores as well as many opportunistic omnivorous species.

1.2.2. AMPHIPODA IN ANTARCTIC BENTHOS

Within Antarctic benthic communities, crustaceans form by far the most species-rich animal group (Arntz et al 1997), and, among crustaceans, amphipods represent the richest groups, with more than 820 recorded species so far (DeBroyer & Jazdzewski 1993, 1996) about 320 of which inhabit Weddell Sea waters. These peracarids have colonized a wide variety of ecological niches, from epontic to below-ground biotopes. They have achieved a successful eco-ethological diversification, occupying apparently all the micro-habitats (De Broyer et al. 2001) and developing various feeding strategies, from suspension-feeding to scavenging on big carrion, as well as specialized modes such as micro-predatory browsing on invertebrate colonies (Dauby et al. 2001a).

“This trophic diversity of amphipods is in a way unique if considering that Antarctic marine fauna is part of the same immense cold-water system (Arntz et al. 1997)”.

Why are amphipod communities so diversified in Antarctic waters? The theme of the high biodiversity of Antarctic fauna and of cold deep-sea fauna in general has been widely debated (see section 1.1.2.1.). Antarctic species richness is attested for amphipods, especially the families Epimeriidae and Iphimediidae, with usually a high degree of endemism. The origin of the Antarctic amphipod fauna and of Iphimediidae in particular, has been discussed by Watling & Thurston (1989). They showed that the most primitive genera were distributed primarily outside Antarctica and were suspected to be relicts of a global distribution, which is in good agreement with the third evolutionary historical model of Crame (1992). Watling & Thurston (1989) suggested that once the Antarctic began to cool (at the Eocene-Oligocene boundary, 38 Ma BP), a radiation occurred in the Southern Ocean, followed by some adaptative morphological reorientations that eventually allowed species to spread outward from the Antarctic. They thus

consider the cooling Antarctic waters to act as an incubator for the Iphimediidae amphipod family.

As suggested for isopods (Clarke & Crame 1989), the expansion of amphipods in the Southern Ocean may represent the filling of an ecological vacuum left by the extinction of the decapods. The taxonomic affinities of the Southern Ocean amphipod fauna were discussed by Knox & Lowry (1977) who suggested this fauna to be a mixture of taxa with different biogeographic origins: (i) a relict of autochthonous fauna, (ii) a fauna which has spread southwards from South America along the Scotia arc (iii) a fauna which has spread northwards from Antarctica along the Scotia arc, and (iv) a fauna derived from adjacent deep-sea basins. The origin of the high amphipod species diversity could also be related to the high oxygen availability in Antarctic waters; indeed Levin & Gage (1998) have showed good correlations between oxygen concentrations and macrobenthos diversity for various bathyal areas. Oxygen availability was also proposed recently to be responsible for the phenomena of extended size spectrum and gigantism observed for the amphipods in the Southern Ocean (Chapelle & Peck 1999) (see Dauby et al. 2001).

The impressive diversity of amphipod taxocoenoses indicates that these crustaceans contribute significantly to biomass and trophodynamics of Antarctic ecosystems. Total biomass data, and *a fortiori* relative data on amphipods are more than scarce, only available for some restricted areas like the eastern Weddell Sea shelf where amphipods should count for about 5% of the benthic biomass (Gerdes et al 1992). Recently Dauby et al (2001b) showed, from an extensive study of gut contents of the most representative species, that their diet was highly complex. On the other hand, based on an exhaustive literature survey (more than 300 references); Dauby et al (2003) tried to delineate the importance of amphipods as potential food for higher trophic levels. About 200 different predators were recorded: 33 invertebrates, 101 fishes, 48 birds and 10 mammals. Using this vast dataset (up to 1500

citations) and published values about predator's standing stocks and feeding rates, an attempt was made to build up a small model, distinguishing between benthic and pelagic species of both amphipods and predators. The total amount of consumed amphipods was estimated to 60 millions of tons per year for the whole Southern Ocean, i.e. the second animal group in importance after euphausiids, the consumption of krill being estimated to about 250 Mt.yr⁻¹ (Everson 1977, Miller & Hampton 1989).

And just to please your eyes, here are pictures of some species that have been considered all along this study...



Paraceradocus gibber (Andres, 1984),
from the family Hadziidae



Djerboa furcipes (Chevreux, 1906),
from the family Eusiridae



Waldeckia obesa (Chevreux, 1905),
from the superfamily Lysianassoidea



Epimeria similis (Chevreux, 1912),
from the family Epimeriidae



Echiniphimedia hodgsoni (Walker, 1906),
from the family Iphimediidae



Epimeria georgiana (Schellenberg,
1931), from the family Epimeriidae

1.3. TROPHIC ECOLOGY INFERRED FROM STABLE ISOTOPE RATIOS

The significance of naturally occurring stable isotopes in ecological research has increased tremendously in the last two decades. While initially restricted to the domain of earth sciences, stable isotope techniques are increasingly being used in physiology, ecology and atmospheric science to investigate questions ranging from the molecular to the ecosystem level (Lajtha & Michener 1994).

1.3.1. THEORY

Isotopes are atoms of the same element which nucleus contains the same number of protons (p), but a different number of neutrons (n), resulting in different atomic masses. There are two types of isotopes: the stable isotopes, which persist in nature, and the radioactive isotopes, which spontaneously degrade.

H, C, N, O and S isotopes are essential in the study of natural processes due to their abundance in Earth systems and their presence in a wide variety of solid, liquid, and gaseous compounds occurring in the biosphere, hydrosphere and lithosphere.

Our work did focus on the study and the analyses of carbon and nitrogen isotopic ratios.

The stable isotopes for carbon and nitrogen are ^{13}C and ^{12}C , and ^{15}N and ^{14}N , respectively. The average natural abundance of these isotopes is given in Table 1.1. In most cases, even for other elements, the light isotope is the more abundant one.

Typically, the value of interest is not the absolute abundance of an isotope in an organism or in a biogeochemical reservoir, but rather the relative

abundances or ratio of “light” to “heavy” isotopes. However those ratios, measured by mass spectrometry, are very small (e.g. the $^{13}\text{C}/^{12}\text{C}$ may vary between 0.010225 and 0.011574). To solve this inconvenient, ratios are measured and reported relative to standard reference materials as delta values:

$$\delta X (\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 10^3$$

where $R = ^{13}\text{C}/^{12}\text{C}$ in the case of carbon and $^{15}\text{N}/^{14}\text{N}$ in the case of nitrogen, i.e. the absolute ratio of the atom occurrence of the “heavy” to “light” isotope, where $X = ^{13}\text{C}$ or ^{15}N , and where the delta values are expressed in parts per thousand or per mil (‰).

Table 1.1.: Average natural abundance of the main stable isotopes of carbon and nitrogen, according to Ehleringer and Rundel, 1989

Element/Isotope	Abundance (atom %)
CARBON	
^{12}C	98.89
^{13}C	1.11
NITROGEN	
^{14}N	99.63
^{15}N	0.37

The internationally accepted stable isotope standards for carbon and nitrogen are Vienna-PeeDee Belemnite (IAEA) and atmospheric nitrogen (Mariotti 1983) respectively.

As the chemical behaviour of atoms is a function of their electronic structure only, isotopes undergo the same reactions. On the other hand, the physical behaviour of atoms is a function of mass, which is determined by the nucleus (since electrons have virtually no mass); therefore isotopes react at different rates. This phenomenon is called “fractionation”. Stable isotope fractionation

in the environment imparts unique isotopic ranges of signatures to various reservoirs (e.g. food sources), as well isotopic shifts that propagate through fluxes between reservoirs.

1.3.2. PATTERNS OF FRACTIONATION IN BIOGEOCHEMICAL PROCESSES

Stable isotopes fractionate during biogeochemical reactions; those small but significant natural variations do not occur randomly but are governed by different physico-chemical processes. Consequently, it is necessary to understand the degree of stable isotope fractionation that occurs during transfer of a chemical substance through an environmental reservoir (e.g. a food web) in order to use stable isotopes as tracers of material transfer.

1.3.2.1. Carbon

The main reaction responsible for the formation of sources with identifiable carbon-isotope signatures in the biosphere is the **photosynthesis**.

Differences in $\delta^{13}\text{C}$ among plants using the Calvin cycle (C_3), Hatch-Slack cycle (C_4) and Crassulacean acid metabolism (CAM) photosynthetic pathways are due to differences in fractionation at the diffusion, dissolution, and carboxylation steps, and are discussed in detail by e.g. O'Leary (1981, 1988a).

Carbon fixed by terrestrial C_3 plants ($\delta^{13}\text{C}$ range: -35 to -21‰) can be distinguished from that fixed by C_4 plants ($\delta^{13}\text{C}$ range: -14 to -10‰). This difference is due to the stronger discrimination against ^{13}C isotopes by the primary CO_2 -fixing enzyme of the C_3 plants: the ribulose biphosphate carboxylase (Rubisco). In C_4 plants, the primary enzyme for CO_2 fixation, the phosphoenolpyruvate carboxylase (PEP) discriminates against ^{13}C in a lesser extent (O'Leary 1981, 1988, Farquhar et al 1989).

However, while marine phytoplankton uses the Calvin cycle as photosynthetic pathway, its isotopic ratio is significantly heavier (-22‰) than that of terrestrial C₃ plants. Such difference is likely to be caused by the use of bicarbonate as a carbon source in marine systems and by the slower diffusion of carbon dioxide in water, which might counteract the discrimination by the enzyme (O’Leary 1988, Boutton 1991, Kelly 1999).

Aquatic plants have been found to show widely varying stable isotope signatures (reviewed by Bouillon, 2002). The major factors influencing the carbon isotopic composition of aquatic plants are the following: the isotopic composition of the substrate, the substrate type (CO₂ or HCO₃⁻) and the water velocity. It should be noted that a few additional factors such as the growth rate and the size and shape of the cells are particularly important for microalgae.

All these differences in ¹³C/¹²C ratios in primary consumers are sufficient enough to influence carbon isotopic composition of their respective consumers and assign them a specific isotopic signature.

1.3.2.2. Nitrogen

In contrast to the numerous studies on the carbon fractionation during primary production, knowledge on fractionation processes during N-assimilation is quite limited. However, nitrogen isotopic composition of primary producers in aquatic as well as in terrestrial systems may give indications about nitrogen sources and transformations.

Kinetic isotope fractionation is associated with most biological reactions involving inorganic nitrogen. These reactions include the assimilation of dissolved inorganic nitrogen (either under the form of nitrates, nitrites or ammonium) by phytoplankton, or bacteria nitrification and denitrification, and N₂ fixation. Generally, the end product is depleted in ¹⁵N relative to the substrate, resulting in an enrichment of the residual substrate pool.

Denitrification seems to be the reaction leading to the largest fractionation effects, probably due to the break of the particularly strong covalent bonds it implies.

As for carbon, a multitude of factors may influence nitrogen fractionation and the numerous studies devoted to this subject have revealed wide variations of nitrogen isotopic ratios with light intensity, species, nitrogen substrate, culture conditions resulting in various fractionation values for algae.

1.3.3. STABLE ISOTOPES IN FOOD WEBS

Standard approaches to food web analysis include gut content analysis, direct observation in the field as well as in the laboratory, and radiotracer techniques, each method having its own advantages and drawbacks (Auel & Werner 2003, Werner et al. 2002). For example, analysis of gut contents involves collecting and dissecting a broad range of organisms to determine food web structure and requires few tools and equipment (Dauby et al 2001). However, some preys are sometimes digested more quickly than others, making identification difficult and bringing biases in the determination of diet composition. Furthermore, gut content is only a snapshot of the diet revealing what the organisms fed on short time before the sampling and may include material which is not really assimilated.

An alternative technique for aquatic food web studies is the use of immunological methods (Theilacker et al. 1993). It involves the development of antisera for whole organisms extracts. It has been shown that the antisera are usually taxon-specific and can trace trophic relationships. For example, immunochemistry has been used successfully to examine predation by the euphausiid *Euphausia pacifica* on early life stages of anchovy (Theilacker et al. 1993). Also, while most immunochemistry studies have focused on identifying animal prey, Haberman et al. (2002) used immunochemical methods to analyze ingestion of the prymnesiophyte *Phaeocystis antarctica*

by Antarctic krill *Euphausia superba*. However, if this method sounds promising, to study ecosystems with a large number of species, it would be prohibitively expensive and time-consuming to check all possible antisera...

Stable isotopes analysis has more recently been used as an alternative, and is some cases, better tool for food web analysis.

Since food sources show considerable variations in their carbon-isotope signatures, the utility of these isotopes for trophic studies hinges on the relationships between the isotope composition of a consumer's diet and that of its tissues.

DeNiro and Epstein (1978a) were pioneers providing evidence that, first, the carbon-isotope composition of a consumer was a direct reflection of its diet and, secondly, that the whole bodies of consumers were enriched in ^{13}C only slightly over their diet (i.e. the fractionation was less than 2‰). Ensuing studies have confirmed Epstein and DeNiro's (1978) findings, for example, with birds (Mizutani et al. 1992, Hobson and Clark 1992a, 1992b, 1993) and mammals (Tieszen et al. 1983, Hobson et al. 1996, Hildebrand et al 1996). This minor stepwise trophic enrichment of the carbon isotope ratio that has been documented limits its use in discriminating trophic levels. However, this characteristic enhances the utility of carbon isotope ratios for tracking carbon sources through a food chain (Peterson & Fry 1987, Michener & Schell 1994). Specifically, since enrichment at each trophic level is small, the carbon isotope signature of secondary and tertiary consumers should reflect the source of carbon at the base of the food chain (reviewed by Kelly, 2000).

As with carbon, DeNiro and Epstein (1981a) found that $\delta^{15}\text{N}$ of a consumer reflects $\delta^{15}\text{N}$ of its diet, but in most cases the whole animal is enriched in ^{15}N relative to the diet. When enrichment occurs, it seems to be due to a preferential excretion of ^{15}N -depleted nitrogen, usually in the form of urea and ammonia and this progressive enrichment increases along advancing

trophic levels (Minagawa and Wada 1984, Peterson and Fry 1987, Ehleringer and Rundel 1989).

Despite the multiple advantages and possibilities offered by the method, the researcher must be aware of its limits such as the isotopic variations in different tissues within an organism, as well as different rates of tissue turnover. Indeed, despite recent advances in stable isotope analysis, relatively few experimental studies have addressed the relationship between the isotopic composition of an animal and its food, and the response time of different tissue types to changes in the isotopic composition of the food source (Gannes et al. 1997). For example, in a feeding study of rodents, Tieszen et al. (1983) found that ^{13}C enrichment for individual tissues fell from hair > brain > muscle > liver > fat after switching the diet from a C_4 corn to a C_3 wheat. Obviously the speed at which isotopic composition changed over time to reflect the new diet depended on tissue type, with the more metabolically active tissues turning over more quickly. More recently, a study of the mysid crustaceans, *Mysis mixta* and *Neomysis integer* in Arctic waters demonstrated experimentally that the isotopic composition in muscle, exuviae, and feces may form a basis for diet reconstruction of mysids (Gorokhova & Hansson 1999).

Stable isotope based trophic studies have been applied successfully to the Antarctic marine communities (Wada et al. 1987; Burns et al. 1998) and particularly to the pelagic fauna and the top predators of the Weddell Sea (Rau et al. 1991a, b, 1992). On the other hand, there is a lack of such studies for Antarctic benthic ecosystems except for some sub-Antarctic Islands (Kaehler et al. 2000) although there subsists many trophic interactions to clarify. Indeed, the previously presumed simplicity of Antarctic food webs (e.g. Heywood and Whitaker 1984) is questionable. Until about 20 years ago the main flow of energy in Antarctic marine environment was considered to

be a food chain directly from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. Heywood and Whitaker 1984), but those simple food chain models do not reflect reality appropriately (Marchant and Murphy 1994). Diatoms constitute the major component of Antarctic marine phytoplankton indeed, but bacterial production - as part of the microbial loop – may attain from 11% (spring, Sullivan et al. 1990) to 76% of primary production (autumn, Cota et al. 1990) The sea-ice community is suspected to be yet another important food source (Marshall 1988; Daly 1990). The complexity of the Antarctic marine food web is now considered to be as high as that of many others in lower-latitude ecosystems (Garrison 1991). Hence we have to deal with the complicated multiple and isotopically contrasting food bases often present in marine environments (Fry 1988; Hobson 1993, Hobson et al. 1995, Marguillier et al. 1997; Lepoint et al. 2000, Nyssen et al. 2002).

1.4. TROPHIC ECOLOGY INFERRED FROM FATTY ACID COMPOSITION

1.4.1. FATTY ACID STRUCTURE

To describe precisely the structure of a fatty acid molecule, one must give the length of the carbon chain (number of carbon atoms), the number of double bonds and also the exact position of these double bonds. Fatty acids (FA) and their acyl radicals are named according to the IUPAC Rules or the Nomenclature of Organic Chemistry (IUPAC). This will define the biological reactivity of the fatty acid molecule and even of the lipid containing the fatty acids studied.

Marine fatty acids are straight-chain compounds with most frequently an even number of carbon atoms. Chain-length ranges commonly between 12 and 24 carbons.

Fatty acids can be subdivided into well-defined categories:

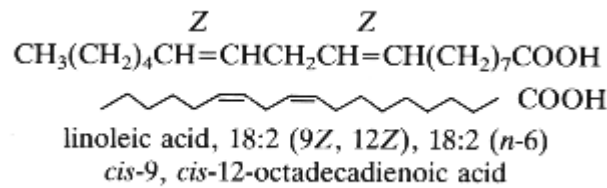
- **Saturated** fatty acids which have no unsaturated linkages

When double bonds are present, fatty acids are denominated unsaturated:

- **Monounsaturated** fatty acids (MUFA) if only one double bond is present.
- **Polyunsaturated fatty acids** (PUFA) if they have two or more double bonds generally separated by a single methylene group (methylene-interrupted unsaturation).

In some animals, but mainly in plants and bacteria, fatty acids may be more complex since they can have an odd number of carbon atoms, or may contain a variety of other functional groups, including **acetylenic** bonds, epoxy-, **hydroxy**- or keto groups and even **ring** structures (cyclopropane, cyclopropene, cyclopentene, furan, and cyclohexyl).

Example:



Nomenclature: The double bonds are counted from the methyl group determining the metabolic family, noted by n-x (n being the total number of carbon, x the position of the first double bond). Thus linoleic acid or octadecadienoic acid is named in the shorthand nomenclature 18:2 (n-6). This compound has 18 carbon atoms, 2 double bonds and 6 carbon atoms from the first double bond. The International Commission on Biochemical Nomenclature agreed to the first form of this nomenclature because of its interest in describing the fatty acid metabolism.

1.4.2. FATTY ACID AS TROPHIC BIOMARKERS

Fatty acids are in many circumstances incorporated into consumers in a conservative manner, thereby providing information on predator-prey relations. Because of biochemical properties and limitations, many dietary fatty acids generally remain intact through digestion, absorption and transport in the bloodstream, and are incorporated into marine animal tissues with little or no modification of the original structure. Therefore these fatty acids are useful as indicators or markers of the dietary source. Combinations of these markers, or the whole suite of fatty acids present, are referred to as the fatty acid signature of an organism (Iverson 1993, Dalsgaard et al. 2003 for review).

Moreover, contrary to the more traditional gut content analyses, which provide information only on recent feeding, FA provide information on the

dietary intake and the food constituents integrated over a longer period of time (St. John and Lund 1996, Kirsch et al. 1998, Auel et al. 2002). This integrating effect helps to resolve the importance of specific prey items and can validate prey utilization strategies based on traditional stomach content analyses (Graeve et al. 1994b). If FA analysis has numerous advantages, it has also its drawbacks. For example, no single FA can be assigned uniquely to any one species and depending on the condition and metabolic strategies of the consumer, FA are not necessarily metabolically stable. In addition, turnover rate of individual FA, can be species-specific and are often linked to the metabolic condition of the organism, and have seldom been quantified (St. John and Lund 1996, Kirsch et al. 1998). Consequently; fatty acids have so far only been used as qualitative and “semi-quantitative” food web markers, the latter in concert with other tracers such as stable isotopes (Kiyashko et al. 1998, Kharlamenko et al. 2001).

Resolution of ecological niches is the strength of the fatty acid trophic markers (FATM) approach and a key to resolve complex trophic interactions. FATM are incorporated largely unaltered into lipid pool of primary consumers.

The concept of FA being transferred conservatively through aquatic food webs was first suggested by Lovern (1935) in a study about copepods. Almost 30 years later, Kayama et al. (1963) performed one of the first experiments demonstrating the transfer of FA through a linear, experimental food web consisting of diatoms, branchiopods and freshwater guppies. The FA profile of the branchiopods and the guppies clearly showed the transfer as well as endogenous modifications of dietary FA. Other studies recognized that the fatty acid composition of zooplankton lipids influenced the fatty acid composition of the blubber lipids of the baleen whales that fed on them (e.g. Ackman and Eaton 1966). However, Sargent et al. (1987) were among the first to suggest the use of marker fatty acids in the study of trophic relationships. Since that time, numerous studies have demonstrated that fatty

acid signatures can be passed from prey to predator, both at the bottom (e.g. Fraser et al. 1989, Graeve et al. 1994) and near the top of the food web (e.g. Iverson 1993, Kirsch et al. 1998, Kirsch et al. 2000, Iverson et al. 2002, Budge et al. 2002). Once fatty acids are characterized in the prey organism, they can be used to trace food webs and diets of predators. For example, fatty acids have been used to study the diets of fish and copepods (e.g. Sargent et al. 1989, Fraser et al. 1989, Graeve et al. 1994b, Graeve et al. 1997, St John and Lund 1996). Fatty acids have also been used to indicate the presence of fish and other preys in the diet of terrestrial and aquatic carnivores (e.g. Rouvinen et al. 1992, Colby et al. 1993), and spatial and temporal differences in diets both within and between marine mammals species (Iverson et al. 1997a, 1997b, Smith et al. 1997).

In recent years, an increasing number of studies have applied this method to identify trophic relationships in various marine ecosystems. In polar areas, a variety of taxa and functional groups have been studied so far: copepods (e.g. Graeve et al. 1994a, Kattner and Hagen 1995, Scott et al. 1999), euphausiids (Hagen and Kattner 1998, Kattner and Hagen 1998, Phleger et al. 1998, Virtue et al. 2000, Stübing et al. 2003; see also Falk-Petersen et al. 2000 for review), amphipods (Graeve et al. 2001, Nyssen et al. in press), Arctic zooplankton (Scott et al. 1999, Falk-Petersen et al. 2002) and benthos in general (Graeve et al. 1997).

The most abundant fatty acids generally considered in lipid studies include:

- Saturated fatty acids: 14:0, 15:0, 16:0, 18:0;
- Monounsaturated fatty acids: 16:1(n-7), 18:1(n-9), 18:1(n-7), 20:1(n-9), 20:1(n-7), 22:1(n-11), 22:1(n-9);
- Polyunsaturated fatty acids: 16:2(n-4), 18:2(n-6), 16:3(n-4), 16:4(n-1), 18:3(n-6), 18:3(n-3), 18:4(n-3), 20:4(n-6), 20:4(n-3), 20:5(n-3), 22:5(n-3), 22:6(n-3).

Among the specific lipid components suggested for use as trophic biomarkers, the fatty acids 16:1(n-7), C16 PUFA and EPA and 18:1(n-7) are

considered indicators of a diatom-based diet (Graeve et al. 1994a, 1997). More specifically, sympagic diatoms constitute the bulk of ice algae, and produce high amounts of EPA (eicosapentanoic acid, 20:5(n-3)) (Falk-Petersen et al. 1998, Scott et al. 1999). In contrast, flagellates usually contain elevated concentrations of DHA (docosahexaenoic acid, 22:6(n-3)) as well as 18:4(n-3) (Graeve et al. 1994a).

Tracking trophodynamic relationships in omnivorous and carnivorous species in general, using FATM, is more complex than for herbivores. Secondary and higher order consumers may also incorporate dietary FA largely unaltered into their lipid reserves, but the signal of herbivory are obscured as the degree of carnivory increases and FA may derive from many different sources (Auel et al. 2002). Markers of herbivory may be replaced by markers of carnivory, reflecting changes in feeding behaviour such as during ontogeny. For example, the fatty acid 18:1(n-9) has been used as an indicator of carnivorous feeding in general (Sargent and Henderson 1986, Graeve et al 1994a, 1997). Another example are the long-chain monounsaturated fatty acids and alcohols 20:1(n-9) and 22:1(n-11) that are biosynthesized *de novo* by herbivorous calanoid copepods. So, these particular monounsaturates have been used to trace and resolve food web relationships at higher trophic levels, for example in hyperiid amphipods, euphausiids and zooplanktivorous fishes that typically consume large quantities of calanoid copepods (e.g. Sargent 1978, Falk-Petersen et al 1987, Hopkins et al. 1993, Kattner and Hagen 1998, Hagen et al. 2001, Auel et al 2002).

In order to obtain more decisive information on diet composition and trophic level using fatty acid composition, ratios of particular FA have also been used to assess the extent to which various species occupy different ecological niches. As diatoms contain high levels of 16:1(n-7) and EPA, whereas dinoflagellates and *Phaeocystis* are usually rich in DHA, the ratios 16:1(n-7)/16:0 and EPA/DHA could allow to differentiate between a diatom-versus a flagellate-based diet (Graeve et al. 1994a, Nelson et al. 2001). Moreover,

high EPA/DHA ratios may indicate an important influence of ice-algal primary production (Falk-Petersen et al. 1998, Scott et al. 1999).

The PUFA/SFA ratio has been used as an indicator of carnivory in Antarctic krill *Euphausia superba* (Cripps and Atkinson 2000). Similarly, the proportion of 18:1(n-7) to 18:1(n-9) (as a marker of primary or heterotrophic bacterial production vs. animal production) was, for example, found to decrease in Arctic benthic organisms when considering a “succession” from suspension feeders via predatory decapods to scavenging amphipods (Graeve et al. 1997) as it has similarly been proposed as a relative measure of carnivory in various groups of marine invertebrates (Auel et al. 1999, 2002, Falk-Petersen et al. 2000).

At higher trophic levels, i.e. in fish and marine mammals, specific FATM are of less evident than in zooplankton and consequently more difficult to interpret. The advancement of multivariate statistical methods of pattern recognition has, however, proven particularly valuable for resolving trophic interactions in these organisms (Smith et al. 1997, Iverson et al. 1997b, 2002, Budge et al. 2002), and we urge that this becomes an integrated tool in future applications of FATM at all trophic levels.

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CHAPTER 2: A STABLE ISOTOPE APPROACH TO THE EASTERN WEDDELL SEA TROPHIC WEB: FOCUS ON BENTHIC AMPHIPODS

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ABSTRACT

Stable isotope ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) analyses were performed in ninety species belonging to different benthic communities sampled in the eastern Weddell Sea. The study focused on the eight amphipods species from which isotopic composition was compared to their respective gut contents previously described. Amphipod stable isotope ratios correspond rather accurately to the trophic classification based on gut contents and attest to their high spectrum of feeding types. Since the fundamental difference between the isotope and the gut content approaches to diet studies is the time scale each method addresses, this coincidence indicates that there would be no significant changes in feeding strategies over time. Three levels of the food web are covered by the eight species and, instead of belonging strictly to one trophic category, amphipods display a continuum of values from the suspension-feeder to scavengers.

2.1. INTRODUCTION

With more than one thousand strictly Antarctic species, the peracarid Crustacea are the most speciose animal group in the Southern Ocean. Among them, the amphipods, with 531 Antarctic species and about 830 spp. in the whole Southern Ocean, are clearly the most diverse. (Klages 1991 ; De Broyer and Jazdzewski 1996 ; De Broyer et al. 1999 ; Gutt et al. 2000). Trophic diversity and species diversity are obviously related. In Antarctic waters, and on Antarctic bottoms, suitable microhabitats for amphipods are numerous and diversified, which allowed them to adopt various life styles: epontic dwellers, (benthic-) pelagic swimmers, walkers, crawlers, burrowers, borers, inquilines in or on different invertebrates. This diversity in microhabitats, associated with the variety of potential food, is likely to be a factor which has favoured the adaptative radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jazdzewski et al. 1996; Dauby et al. 2001; De Broyer et al. 2001). Furthermore, peracarid crustaceans are important food sources for many Southern Ocean benthic invertebrates (e.g. Dearborn 1977; Dearborn et al. 1991; McClintock 1994), for demersal and benthic fishes (e.g. Kock 1992; Olaso et al. 2000), for many of birds (e.g. Ainley et al. 1992; Cherel and Kooyman 1998; Jazdzewski and Konopacka 1999), and for marine mammals (e.g. Dearborn 1965; Green & Burton 1987). Regarding total energy flow in the eastern Weddell Sea shelf ecosystem, they are among the key taxa in the benthic sub-system (Jarre-Teichmann et al. 1997). The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their role in Antarctic trophodynamics.

Compared to observational techniques in studies of animal diet (i.e. gut content examination), stable isotope ratio analyses provide signatures based on actual food assimilation and are integrated over a period corresponding to the turnover time of the analysed tissues (Tieszen et al. 1983; Hobson et al.

1996, 1997). The technique relies upon the direct relationship between the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of animals and those of their diets (De Niro and Epstein 1978, 1981; Peterson and Fry 1987). Changes in ratios (i.e. fractionation) occur through metabolic processes which cause the lighter isotope to be preferentially lost and the heavier one to be retained. As a result, the stable isotope composition of a consumer is indicative of and heavier than that of its prey. Within a food chain, $\delta^{15}\text{N}$ displays a stepwise increment of about 3‰ at each successive trophic level (Minagawa and Wada 1984; Hobson and Welch 1992; Michener and Schell 1994) and is generally used to predict organism's trophic level. Likewise, animal carbon isotope values, closer to that of the diet, allow determining the original source of organic matter to the food web. Isotopes have been successfully applied to the Antarctic Ocean (Wada et al. 1987; Burns et al. 1998) and particularly to the pelagic fauna and the top predators of the Weddell Sea (Rau et al. 1991a, b, 1992). On the other hand, there is a lack of such studies for Antarctic benthic ecosystems except for some sub-Antarctic Islands (Kaehler et al. 2000).

The previously presumed simplicity of Antarctic food webs is questionable. Until about 20 years ago the main flow of energy in Antarctic marine environment was considered to be a food chain directly from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. Heywood and Whitaker 1984) but those simple food chain descriptions are no longer useful (Marchant and Murphy 1994). Indeed, diatoms are recognized as major components of Antarctic marine phytoplankton but, as the microbial loop – in the Weddell-Scotia Sea bacterial production ranged from 11% of primary production in spring (Sullivan et al. 1990) to 76% of primary production in autumn (Cota et al. 1990) – other production pathways have to be considered. The sea-ice community for example is suspected to be an important food source for some Southern Ocean invertebrates (Marschall 1988; Daly 1990). The complexity of the Antarctic marine food web is now

considered to be as high as that of many others in lower-latitude ecosystems (Garrison 1991). Hence we have to deal with the complicated multiple and isotopically contrasting food bases often present in marine environments (Fry 1988; Marguillier et al. 1997; Lepoint et al. 2000).

Using carbon and nitrogen stable isotope analyses, our aim was to determine the trophic position of selected amphipod species in the eastern Weddell Sea food web and to combine our results with gut content analyses carried out by Dauby et al. (2001).

2.2. MATERIAL AND METHODS

2.2.1. SAMPLING AND STORAGE

During the expedition ANT XIII/3 (EASIZ I) of R.V. *Polarstern* to the eastern Weddell Sea in 1996, more than 500 samples referring to 110 benthic invertebrate species (from sponges to finfish) were collected with either Agassiz, bottom, benthopelagic trawls or with traps. Among these organisms, the following amphipod species were determined: *Ampelisca richardsoni* Karaman, 1975; *Waldeckia obesa* (Chevreux, 1905); *Parschisturella carinata* (Schellenberg, 1926); *Orchomenella* cf. *pinguides* (Walker, 1903); *Iphimediella cyclogena* K. H. Barnard, 1930; *Tryphosella murrayi* (Walker, 1903); *Eusirus perdentatus* Chevreux, 1912 and *Epimeria similis* Chevreux, 1912. Additional suspended particulate organic matter (SPOM) composed mainly of diatoms (*Corethron* sp. and *Chaetoceros* sp.), and zooplankton samples were collected from the onboard seawater. All samples were immediately freeze-dried and stored until their preparation for analyses.

2.2.2. ISOTOPIC ANALYSIS

When possible, muscle tissues or soft body parts from 5 individuals of every sampled species (except from the amphipod *E. similis*, n=1) were sampled and ground with mortar and pestle into a homogenous powder. From one hundred and ten species initially analysed, ninety species provided valuable results. In amphipods, isotope ratios were determined individually in each specimen, whereas in other invertebrate species, five individuals were pooled prior to analysis.

The lipids were not extracted from the tissues. Stable carbon and nitrogen isotope ratios were analysed with an Optima (Micromass, UK) continuous flow isotope ratio mass spectrometer (CF-IRMS) directly coupled to a N-C elemental analyser (Fisons, UK) for combustion and automated analysis. Isotopic ratios are expressed in δ notation as the proportional deviation of the sample isotope ratio from that of an international standard according to the following formula:

$$\delta X (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

Where X is ^{13}C or ^{15}N , R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, and the appropriate standards were Vienna Peedee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Intercomparison materials were IAEA-N1 ($\delta^{15}\text{N} = +0.4 \pm 0.2\text{‰}$) and IAEA CH-6 (sucrose) ($\delta^{13}\text{C} = -10.4 \pm 0.2\text{‰}$). As recommended by Pinnegar & Polunin (1999), when samples were acidified to eliminate carbonates, $^{15}\text{N}/^{14}\text{N}$ ratios were measured before acidification due to significant modifications of nitrogen ratios after HCl addition (Bunn et al. 1995). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.5 and 0.4‰ for carbon and nitrogen, respectively.

Based on findings of several authors (e.g. Minagawa and Wada 1984; Wada et al. 1987; Hobson and Welch 1992; Michener and Schell 1994; Hobson et al. 1995), a "per-trophic-level" ^{15}N enrichment factor of about 3.0 ‰ was applied to obtain trophic level estimates according to the relationship:

$$TL = (D - 3.1)/3.0 + 1$$

Where D is the $\delta^{15}\text{N}$ value of the organism, 3.1 refers to the mean value of SPOM, and TL is the organism's trophic level (see Table 1).

Parametric tests were used to compare isotope ratios between different taxa. Normality of the data was checked by the Kolmogorov-Smirnov test followed by ANOVA and post-hoc comparisons of means. Correlations between data were explored by the Spearman rank coefficient. A significance level of $p < 0.01$ was used in all tests (Scherrer 1984).

The calculation of the gut content percentages displayed in Table 2.1 are described in Dauby *et al.* (2001).

Table 2.1. Trophic types based on gut content analyses (modified from Dauby *et al.* 2001), $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N ratios (mean \pm SE) and estimated trophic level (TL) (from Hobson and Welch 1992); n: number of samples.

Species	Trophic types	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	TL
<i>Ampelisca richardsoni</i> (n = 5)	SUSPENSION FEEDER (diatoms (54%), undetermined organic matter (36%), Porifera (7%), Crustacea (3%))	5.4 \pm 0.4	-27.1 \pm 0.9	6.6 \pm 0.6	2.1
<i>Eusirus perdentatus</i> (n = 5)	PREDATOR (Crustacea (44%), mineral particles (27%), unidentified organic matter (25%), Polychaeta (4%))	5.1 \pm 1.2	-23.7 \pm 1.9	9.3 \pm 1.5	3.0
<i>Epimeria similis</i> (n = 1)	PREDATOR (Cnidaria (63%), Porifera (14%), Polychaeta (9%), diatoms (9%), others (5%))	5.6	-25.1	10.1	3.3
<i>Orchomenella cf pinguides</i> (n = 5)	DEPOSIT FEEDER (Crustacea (36%), Porifera (24%), diatoms (24%), unidentified organic matter (16%))	7.0 \pm 0.4	-22.3 \pm 1.8	10.9 \pm 0.3	3.6
<i>Iphimediella cyclogena</i> (n = 5)	PREDATOR (Holothurioidea (70%), Polychaeta (20%), unidentified organic matter (10%))	4.0 \pm 0.3	-25.9 \pm 1.1	11.2 \pm 0.5	3.7
<i>Tryphosella murrayi</i> (n = 5)	SCAVENGER (carion (47%), Crustacea (43%), Polychaeta (5%), others (5%))	5.5 \pm 0.2	-22.5 \pm 0.8	11.4 \pm 0.8	3.8
<i>Waldeckia obesa</i> (n = 5)	SCAVENGER (carion (85%), diatoms (5%), mineral particles (5%), Porifera (5%))	6.7 \pm 0.5	-22.8 \pm 0.7	11.6 \pm 0.3	3.8
<i>Parschisturella carinata</i> (n = 5)	No gut content data but considered as SCAVENGER	6.9 \pm 1.1	-21.1 \pm 2.1	11.8 \pm 0.7	3.9

2.3. Results

The ranges of isotope ratios of each taxon - grouped by phylum, class or order following the number of samples - as well as that of suspended matter are presented in Figs 2.1 and 2.2. The first plan of gathering the taxa by order had to be abandoned because of the lack of significance of statistical tests. Our isotopic analyses revealed a considerable range in both ^{13}C and ^{15}N values for benthic components.

Stable carbon isotope ratios ranged from -32‰ for the SPOM to -16.1‰ for the anthozoan *Thouarella* sp. Considerable overlap in ^{13}C values appears throughout the food web and the trophic enrichment between trophic levels is not really obvious. ^{15}N values were generally less variable than ^{13}C and a step-wise increase with trophic level ranged from 2.6‰ for SPOM to 16.1‰ for the fish *Pogonophryne barsukovi* (Artedidraconidae) suggesting a food web composed of about 5 trophic levels (see Minagawa and Wada 1984; Wada et al. 1987; Hobson and Welch 1992; Michener and Schell 1994; Hobson et al. 1995). As expected, SPOM isotopic ratios ($n = 3$) are the lowest ranging from -32 to -28.7‰ in $\delta^{13}\text{C}$ and from 2.6 to 3.9‰ in $\delta^{15}\text{N}$. For both isotopes, amphipod ranges are among the widest (from -27.8 to -19.6‰ in $\delta^{13}\text{C}$ and from 5.8 to 12.9‰ in $\delta^{15}\text{N}$) together with those of anthozoans and echinoderms.

Unfortunately, in this study, the isotopic ratios of some groups can not be discussed because of their poor sampling, for example, isopods are represented by one single species.

Fig. 2.1. Range of $\delta^{13}\text{C}$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Pol. Sedentaria = Polychaeta Sedentaria; Pol. Errantia = Polychaeta Errantia. Numeral between brackets indicates the amount of analysed species.

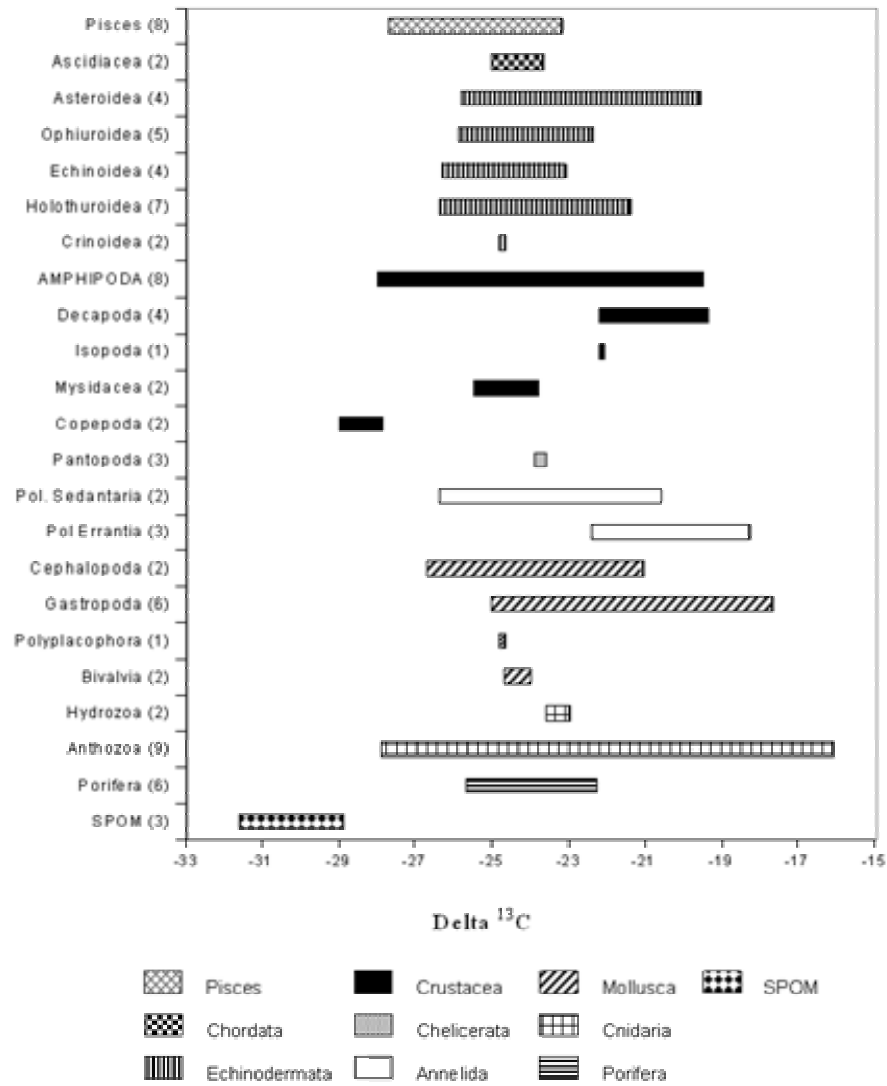
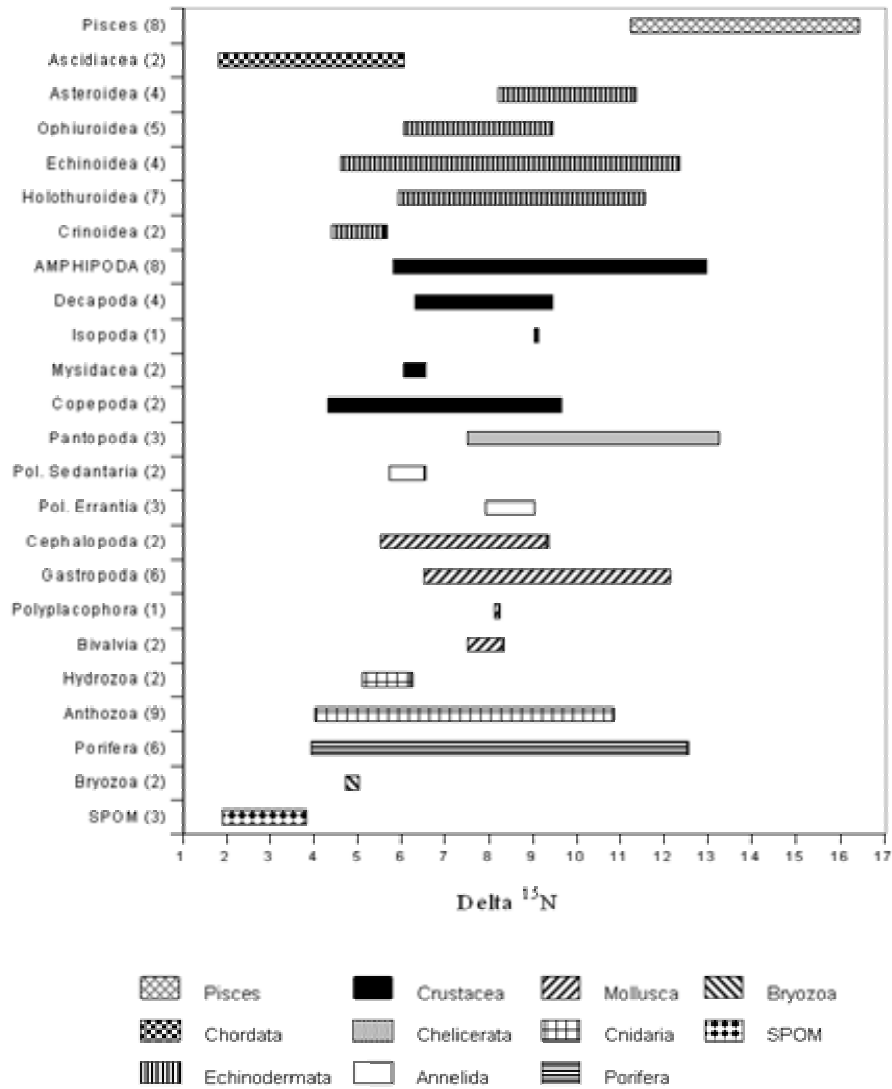
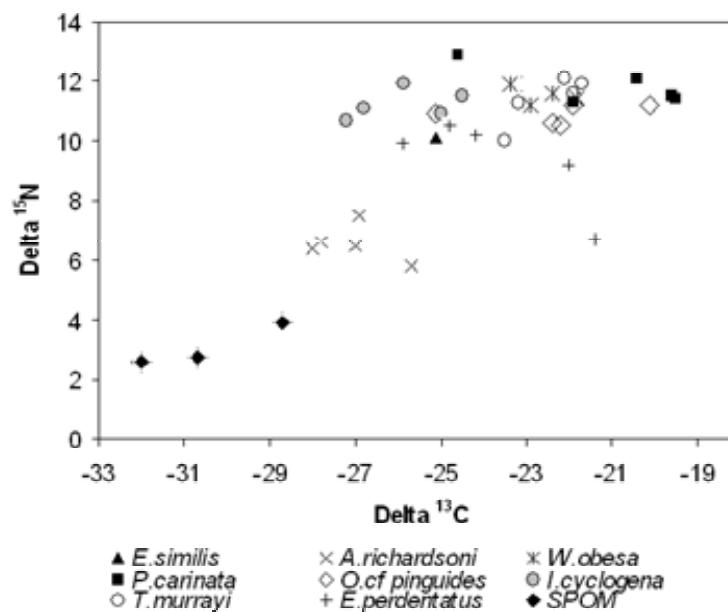


Fig. 2.2. Range of $\delta^{15}\text{N}$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Pol. Sedentaria = Polychaeta Sedentaria; Pol. Errantia = Polychaeta Errantia. Numeral between brackets indicates the amount of analysed species.



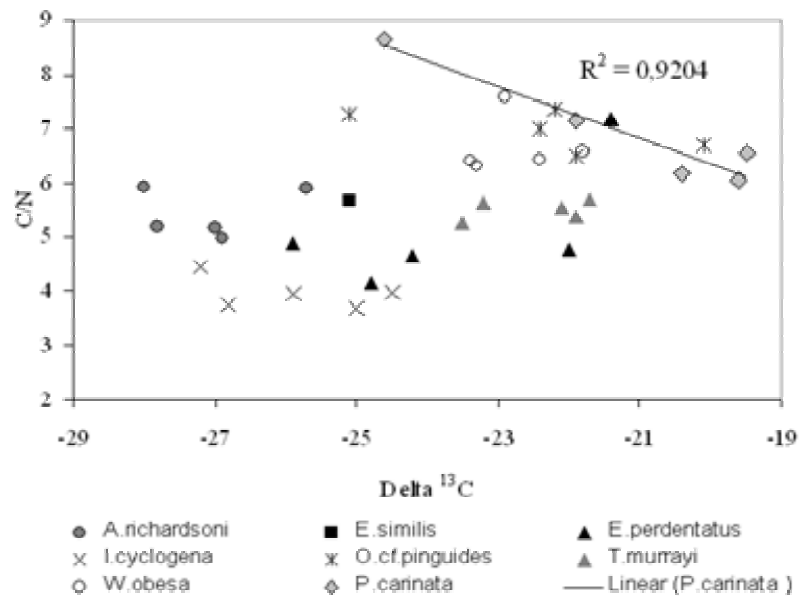
The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in amphipods are presented in Fig 2.3. Displaying the lowest δ ($\delta^{13}\text{C} = -27.1 \pm 0.9\text{‰}$; $\delta^{15}\text{N} = 6.6 \pm 0.6\text{‰}$), *Ampelisca richardsoni* values are closest to those of SPOM and are significantly different from values of all the other species (ANOVA $p < 0.01$) except from *Epimeria similis* and *Iphimediella cyclogena* $\delta^{13}\text{C}$. Both latter species present similar $\delta^{13}\text{C}$ but their nitrogen ratios are significantly different from each other (ANOVA $p < 0.001$). *Eusirus perdentatus* $\delta^{15}\text{N}$ values differ significantly from all other species nitrogen ratios except from the single *E. similis* value. Unlike its $\delta^{13}\text{C}$, *I. cyclogena* $\delta^{15}\text{N}$ values belong to the highest with those of *Orchomenella* cf. *pinguides*, *Waldeckia obesa*, *Tryphosella murrayi* and *Parschisturella carinata*. Furthermore these four latter species stable isotope ratios are not significantly different from each other, neither for the carbon nor for the nitrogen.

Fig. 2.3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values (‰) in SPOM and in amphipods from the eastern Weddell Sea shelf.



When amphipods $\delta^{13}\text{C}$ are compared to their respective C/N ratio, no correlation appears except with one species: *P. carinata*, which displays a significant decrease of $\delta^{13}\text{C}$ with C/N ratio increase (Fig. 2.4).

Fig. 2.4. Relationship between the $\delta^{13}\text{C}$ (‰) and the C/N ratio for amphipod from the eastern Weddell Sea shelf. The displayed regression involves only data from the species *P. carinata*.



2.4. Discussion

The SPOM isotope data are typical of high-latitude northern and southern hemisphere food webs with ^{13}C and ^{15}N -depleted food bases (Wada et al. 1987; Schell and Ziemann 1988; Saupe et al. 1989). More enriched isotopic ratios have been recorded in Antarctic POM but only in fraction samples in or closely associated with sea ice (Rau et al. 1991a; Hobson et al. 1995). Even if there isn't any sea ice POM available for this study, the high values displayed by some sponge species (-22.3 and 12.5 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

respectively) compared to SPOM ratios could reflect an assimilation of sea ice POM by these benthic suspension-feeders. Indeed, by a process of coagulation primarily determined by the stickiness of the cells, many of the dominant ice algae form aggregates which are subject to rapid sedimentation (Riebesell et al. 1991). Another hypothesis to explain such great enrichment between POM and POM grazers would be the assimilation by suspension-feeders of benthic resuspended organic matter originate from a strong microbial loop - the period of sampling (post-bloom, late-summer period) corresponding to its maximal activity (Karl 1993) - through which fixed carbon is first cycled through flagellates and microzooplankton before being consumed. A greater enrichment of benthic organisms due to the assimilation of resuspended and microbially reworked organic matter has already been suggested by Hobson et al. (1995) in an Arctic polynia food web.

Within amphipod species, and particularly for *Orchomenella* cf. *pinguides*, *Eusirus perdentatus* and *Parschisturella carinata*, $\delta^{13}\text{C}$ values were generally more variable than ^{15}N values as observed in most taxa ^{13}C values (see Fig 2.3, Table 2.1). As lipids - both N- and ^{13}C -poor- were not extracted prior to analysis, the intraspecific variation of amphipod $\delta^{13}\text{C}$ could be attributed to the individual differences in concentration of isotopically lighter lipids (DeNiro and Epstein 1977; Tieszen et al. 1983; Wada et al. 1987; Pinnegar and Polunin 1999). There is, however, no significant correlation between amphipods biomass ^{13}C and their biomass C/N, except in one species, *P. carinata* (Fig.2.4). For this species only, the intraspecific variation of the $\delta^{13}\text{C}$ could be attributed to a difference of lipid content between individuals (Rau et al. 1991; 1992).

Few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods do (Figs.2.1 and 2.2). Considerably wide ranges of $\delta^{15}\text{N}$ has already been recorded for pelagic amphipod species from the same sampling area and it has been interpreted as a sign of "diverse feeding strategies and trophic roles within this group" (Rau et al. 1991a). In the present study, the widest ranges of isotopic ratios are displayed by anthozoans, poriferans (for

nitrogen) and amphipods, although the former groups represent higher taxonomic entities. Indeed, our data indicate that benthic amphipods live at many levels of the food web, from the base (*A. richardsoni*) to the top (*P. carinata*), see Fig.2.3. The step-wise increase of $\delta^{15}\text{N}$ with trophic level displayed by the eight amphipod species (see Table 2.1) suggests coverage of approximately 3 of the 5 levels of the food web. Except *Ampelisca richardsoni* which is clearly isolated from the other species at the second trophic level, instead of belonging to a definitive trophic type, amphipods occupy a continuum between the third and the fourth level. This may indicate opportunistic amphipod feeding behaviour (at least for the sampled species).

Our trophic characterization of amphipod based on isotopic values coincides quite well with the trophic classification based on gut contents analyses of Dauby et al. (2001), see Table 2.1. Since the fundamental difference between the isotope and the stomach content approach to diet studies is the time scale each method addresses, this coincidence indicates that there are no distinct changes in feeding strategies over time. The low $\delta^{13}\text{C}$ ($-27.1 \pm 0.9\text{‰}$) and $\delta^{15}\text{N}$ ($6.6 \pm 0.6\text{‰}$) values of *A. richardsoni* which are close to SPOM isotopic ratios ($\delta^{13}\text{C} = -30.5 \pm 1.7\text{‰}$; $\delta^{15}\text{N} = 3.1 \pm 0.7\text{‰}$) confirm that *A. richardsoni* is suspension-feeding on predominantly planktonic items. Further evidence is given by *Ampelisca* lipids, which consist mainly of marked fatty acids of planktonic origin (Graeve et al. in press). Klages and Gutt (1990) consider *E. perdentatus* as a passive predator which preys on various organisms from different trophic levels as polychaetes, amphipods or other smaller crustaceans. Their conclusions didn't only coincide with results of gut content analyses (Dauby et al. 2001) but *E. perdentatus* opportunistic trophic behaviour is also confirmed by its scattered isotopic ratios. Furthermore, according to Graeve et al. (in press) the lack of specialisation neither in the lipid accumulation nor in fatty acid biosynthesis observed for *E. perdentatus* supports this feeding opportunism hypothesis.

The quite high nitrogen ratios of *Iphimediella cyclogena* is amazing as its diet seems to be mainly composed of holothurian tissues considered for the most as suspension- or deposit-feeders (Table 2.1). Antarctic sea cucumbers isotopic values, however, are also higher than expected (Figs 2.1 & 2.2). This may indicate significant microbial or meiofaunal pathways in the organic matter cycle.

Species displaying the highest isotopic values: *Waldeckia obesa*, *Tryphosella murrayi*, *O. cf. pinguides* and *P. carinata* appear to share the same necrophagous trophic behaviour. The carbon and nitrogen isotopic compositions of *W. obesa* and *T. murrayi* are the closest and these data are supported by the high similarity of their diet where carrion-derived organic matter is a major item (e.g. Presler 1986; Dauby et al. 2001). As noticed by Graeve et al. (in press), the fatty acid composition of *W. obesa* is unique since it is by far dominated by oleic acid (nearly 50% of total fatty acids). Lipid-rich fishes as potential food items are known to contain high amounts of this fatty acid (Hagen et al. 2000) but not as high as found for *W. obesa*. *O. cf. pinguides* gut content analyses suggest that this species (at least in this sampling period) is a deposit-feeder. Its rather high isotopic ratios could be explained by the crustacean remains which form almost 40% of its diet. For *P. carinata*, no gut content data are available, but its common occurrence in baited traps, the feeding experiments performed with living specimens in aquaria (Scailteur and De Broyer unpubl.) and the high isotopic ratios would suggest a scavenging trophic behaviour.

In conclusion, the combination of both techniques - and eventually a third as introduced with fatty acid analysis - allows characterizing amphipod trophic status with more accuracy. Some species are rather specific in their diet selection as the suspension-feeder *A. richardsoni*, but the continuum of values displayed by the other species suggests some trophic opportunism and the potential to adapt their diet to food availability in many amphipods. Our results are preliminary and have to be validated by additional analyses with

larger samples of species representative of the Weddell Sea benthic amphipod community. Furthermore, controlled feeding experiments with living Antarctic amphipods could provide more insight in fractionation factors (Gannes et al. 1999).

Acknowledgements

We would like to thank Prof. W. Arntz (AWI, Bremerhaven) for his invitation to participate to the EASIZ cruises, to Officers and Crews of the R.V. *Polarstern*, and Colleagues of the AWI (Bremerhaven, Germany), who helped in collecting and sorting samples. Dr Y. Scailteur (IRScNB) is acknowledged for his huge work in gut content analyses. The first author received a grant from the Belgian "Fonds de la Recherche pour l'Industrie et l'Agriculture" (FRIA). The present research was performed under the auspices of the Scientific Research Programme on Antarctic (Phase IV) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC contract n° A4/36/BO2).

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CHAPTER 3: TROPHIC POSITION OF ANTARCTIC AMPHIPODS - ENHANCED ANALYSIS BY A 2-DIMENSIONAL BIOMARKER ASSAY

After Nyssen F, Brey T, Dauby P, Graeve M (2005) Marine Ecology
Progress Series, in press

ABSTRACT

The discrepancy between the ecological significance of amphipods in the Antarctic and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their trophic status in this ecosystem. Twelve amphipod species from suspension-feeder to scavenger have been considered in this study. Our objective was to investigate whether the combination of fatty acid and stable isotope signatures into a 2-dimensional trophic biomarker assay would increase accuracy in the identification of Antarctic benthic amphipod trophic position. Amphipod isotopic averages ranged from -29.3‰ ($\delta^{13}\text{C}$) and 4.1‰ ($\delta^{15}\text{N}$) for the suspension-feeder *Ampelisca richardsoni*, to -21.7‰ ($\delta^{13}\text{C}$) and 11.9‰ ($\delta^{15}\text{N}$) for the high predator *Iphimediella* sp. Cluster analysis of the fatty acid composition separated the amphipod species into 4 trophic groups; suspension feeders, macro-herbivores, omnivores and scavengers. The suspension feeder was isolated due to an important proportion of 18:4(n-3), fatty acid biomarker of phytoplankton. Macro-herbivores were found to rely heavily on macroalgal carbon, containing a high percentage of arachidonic acid 20:4(n-6). Scavenger amphipods revealed a unique fatty acid composition dominated by one single fatty acid, 18:1(n-9), probably the result of a very intensive de novo biosynthesis to cope with starvation periods. Our data emphasize the need to combine different types of information to be able to draw the right conclusions regarding trophic ecology. Indeed, in some cases, the exclusive use of one type of tracing method, fatty acids or stable isotopes, would have lead to misleading/false conclusions in the trophic classification of amphipods. Therefore a 2-dimensional biomarker assay is a useful tool to elucidate the trophic positions of benthic amphipods.

KEY WORDS: 2-dimensional biomarker, trophic relationships, stable isotopes, fatty acids, Amphipoda, Antarctic ecology

3.1. INTRODUCTION

In the Southern Ocean, amphipod crustaceans are among the most speciose animal group in the zoobenthos. About 530 species have been recorded as strictly Antarctic species and more than 830 species have been described so far for the whole Southern Ocean (Klages 1991, De Broyer & Jazdzewski 1996, De Broyer et al. 1999, 2003a, b, Gutt et al. 2000). It is commonly assumed that species and trophic diversity are related (Ulanowicz 2000, Dauby et al. 2001b). Also, in Antarctic waters and on Antarctic bottoms, amphipods have developed a rich variety of life styles: epontic dwellers, (benthic-) pelagic swimmers, walkers, crawlers, and burrowers. They occupy many niches reserved for decapod crustaceans in other systems (Dauby et al. 2001a, b, De Broyer et al. 2001). This diversity in life style, associated with the variety of available food, is likely to be a factor which has favoured the adaptative radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jazdzewski et al. 1996, De Broyer et al. 2001, Dauby et al. 2001b). Regarding total energy flow in the eastern Weddell Sea shelf ecosystem, Amphipods are among the key taxa in the benthic sub-system (Jarre-Teichmann et al. 1997, Dauby et al. 2003).

Biomarkers such as fatty acids and stable isotopes have been used successfully to identify trophic relationships in marine food webs (Hobson et al. 1995, Lepoint et al. 2000, Graeve et al. 2001, Auel et al. 2002, Nyssen et al. 2002). Fatty acids are the primary constituents of most lipids. They generally remain intact through digestion and can be deposited in the consumer's tissue with minimal modification from diet and in a predictable way (Lee et al. 1971). Certain fatty acids have specific known sources and can act as biomarkers. These features make fatty acids a potential food chain tracer in marine ecosystems, which has shown its suitability in various studies (Sargent 1976, Sargent & Henderson 1986, Graeve et al. 2001, Iverson et al. 2002, Dalsgaard et al. 2003).

Stable isotope ratios also provide signatures based on actual food assimilation but are integrated over a period corresponding to the turnover time of the analysed tissues (Tieszen et al. 1983, Hobson et al. 1996, 1997). The technique relies upon the direct relationship between the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of animals and those of their diets (De Niro & Epstein 1978, 1981, Peterson & Fry 1987). Changes in ratios (i.e. fractionation) occur through metabolic processes, which cause change in the relative proportions of stable isotopes. As a result, the stable isotope composition of a consumer is indicative of and in general heavier than that of its prey. The more conservative transfer of carbon isotopic compositions (0.5‰–1‰ enrichment per trophic transfer) can be useful to trace two food sources with clear differences in their $\delta^{13}\text{C}$ values whereas nitrogen ratios (3‰–4‰ enrichment per trophic transfer) are most frequently used as trophic position indicators (Minagawa & Wada 1984, Hobson & Welch 1992, Michener & Schell 1994, Lepoint et al. 2000). However, it must be considered, that fractionation is not constant and many factors can cause variation (Gannes et al. 1997), e.g. species (e.g. De Niro & Epstein 1981), food source (Fantle et al. 1999), nitrogen dietary content (Adams & Sterner 2000) or nutritional or hydric stress (Hobson et al. 1993). Despite those problems, isotopes have been successfully applied to the Antarctic trophic web (Wada et al. 1987, Burns et al. 1998) and particularly to the pelagic fauna and the top predators of the Weddell Sea (Rau et al. 1991a, b, 1992, Schmidt et al. 2003). Only a few stable isotopic studies have been focussed on benthic communities so far (Dunton 2001, Nyssen et al. 2002). Likewise, there are limited lipid studies of Antarctic benthic amphipods (Nelson et al. 2001, Graeve et al. 2001). More work has been conducted in the Arctic (Hobson et al. 1995, Auel et al. 2002) and on Antarctic pelagic amphipods, e.g. *Themisto gaudichaudii* (Reinhardt & Van Vleet 1986, Hagen 1988, Phleger et al. 1998).

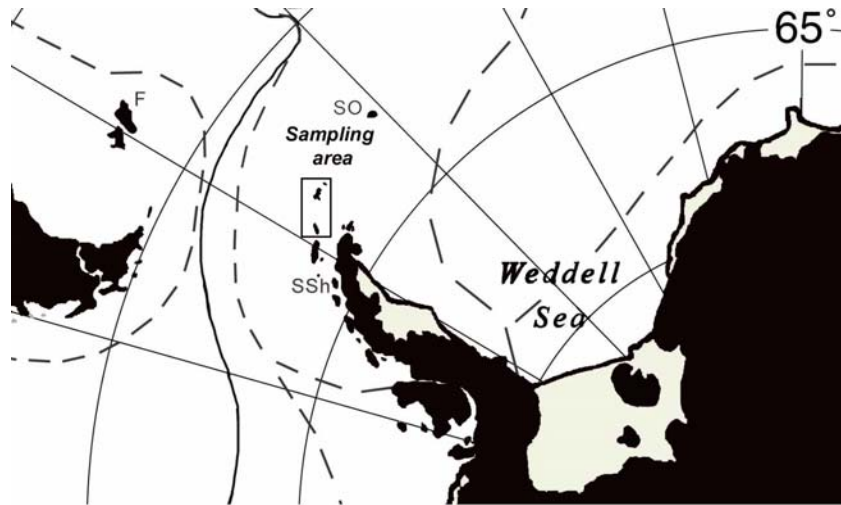
The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their share in Antarctic trophodynamics. Furthermore, the profusion of amphipod species and the variability of their trophic spectrum in the Southern Ocean calls for a more systematic and efficient approach towards this aspect of their ecology. Our study investigates whether the combination of fatty acid and stable isotope signatures into a 2-dimensional trophic biomarker will increase accuracy in the identification of Antarctic benthic amphipod trophic position.

3.2. METHODS

3.2.1. SAMPLING AND STORAGE

The amphipods *Waldeckia obesa* (Chevreux 1905), *Abyssorhomene plebs* (Hurley 1965), *Eurythenes gryllus* (Lichtenstein 1822), *Pseudorhomene coatsi* (Chilton 1912), *Epimeria similis* (Chevreux 1912), *Epimeria georgiana* (Schellenberg 1931), *Iphimediella* sp, *Echiniphimedia hodgsoni* (Walker 1906), *Eusirus perdentatus* (Chevreux 1912), *Djerboa furcipes* (Chevreux 1906) and *Ampelisca richardsoni* (Karaman 1975) were caught during the cruises ANT XIX/3-4 (ANDEEP I-II), 23 January to 1 April 2002 (De Broyer et al. 2003) with RV Polarstern to the Antarctic Peninsula (Fig. 1). The animals were taken from various depths by different gear: Agassiz-trawls, bottom-trawls and autonomous traps. Immediately after sampling, individuals were sorted into species and kept for several hours in aquaria. Thereafter, individuals dedicated to isotope analyses were rinsed in distilled water and transferred into glass vials. Specimens for lipid analysis were transferred into glass vials and covered with dichloromethane:methanol (2:1, by vol.) All samples were stored at -30°C until analysis at the Alfred Wegener Institute at Bremerhaven.

Fig.3.1. Detailed map of the Antarctic Peninsula and the sampling area: F—Falklands, SO—South Orkneys, SSh—South Shetlands.



3.2.2. STOMACH CONTENT ANALYSIS

Gut contents of 20 specimens from each species preserved in 4% formaldehyde solution were examined. The digestive tract was removed from the animal, opened and the content was spread on a micro slide. The slide was examined microscopically (Leica DMLB with reflection contrast system) and every food item was determined as precisely as possible. Additional data were taken from Nyssen et al. (2002) and Dauby et al. (2001b) where the methodological details are described. Observations of feeding behaviour of the various amphipod species in aquaria provided further information on diet and feeding.

3.2.3. LIPID ANALYSIS

Lipid analyses carried out on all sampled amphipod species (n=11). Fatty acid data from Graeve et al. (2001) referring to the species *A. richardsoni*, *E.*

hodgsoni, *Oradarea edentata*, *E. georgiana* (one specimen) and *E. perdentatus* were added to our data set for comparison.

Samples stored in chloroform:methanol (2:1 by vol.) were evaporated with nitrogen to dryness and subsequently lyophilised for 48 h. Dry mass (DM) was determined gravimetrically. Total lipid mass (TL) was measured gravimetrically after lipid extraction from the freeze-dried samples using dichloromethane:methanol (2:1 by vol.), essentially after Folch et al. (1957). Fatty acid composition was analysed by gas-liquid chromatography (Kattner & Fricke 1986). Fatty acids of the total lipid extracts were converted to their methyl esters by transesterification in methanol containing 3% concentrated sulphuric acid at 80°C for 4 hours. After extraction with hexane, fatty acid methyl esters were analysed with a Hewlett-Packard 6890 Series gas chromatograph with a DB-FFAP fused silica capillary column (30 m x 0.25 mm inner diameter; 0.25 µm film thickness) using temperature programming (160-240°C at 4°C min⁻¹, hold 15 min). For recording and integration Class-VP software (4.3) (Shimadzu, Germany) was used. Fatty acids were identified with commercial and natural standard mixtures and if necessary, additional confirmation was carried out by gas chromatography-mass spectrometry.

3.2.4. STABLE ISOTOPE ANALYSIS

Carbon and nitrogen isotopic ratios were measured in all sampled amphipod species (n=11, no isotopic data available for *O.edentata*) as well as in the brown algae *Desmarestia mensiezii*. Isotopic data for suspended particulate organic matter (SPOM) are from Nyssen et al. (2002). Muscle tissues or whole animals of small species were dried and ground with mortar and pestle into a homogenous powder. Isotopic ratios were measured individually in each specimen. Stable carbon and nitrogen isotope ratios were analysed with a nitrogen-carbon elemental analyser (Fisons, UK) directly coupled to an Optima (Micromass, UK) continuous flow isotope ratio mass spectrometer

(CF-IRMS) for combustion and automated analysis. Isotopic ratios are expressed in δ values as the proportional deviation of the sample isotope ratio from that of an international Vienna Pee Dee Belemnite (V-PDB) standard according to the following formula:

$$\delta X (\text{‰}) = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000,$$

where X is ^{13}C or ^{15}N , R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, and the appropriate standards were Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Intercomparison materials were IAEA-N1 ($\delta^{15}\text{N} = +0.4 \pm 0.2\text{‰}$) and IAEA CH-6 (sucrose) ($\delta^{13}\text{C} = -10.4 \pm 0.2\text{‰}$). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.3‰ for both carbon and nitrogen.

3.2.5. DATA ANALYSIS

Multivariate analyses of the fatty acid composition were performed for all individuals using the program PRIMER (Plymouth Routines in Multivariate Ecological Research), Version 5 (Clarke & Warwick 1994). Hierarchical clustering and multi-dimensional scaling (MDS) were performed based on a Bray-Curtis similarity coefficient applied to untransformed percentage composition data. No transformation was applied to the data set, because those fatty acids that contribute only to a small percentage of the total composition did not feature heavily in the diet. Giving artificial weight to these minor fatty acids by applying a transformation would therefore be inappropriate. Data from Graeve et al. (2001) referring to the species *A. richardsoni*, *E. hodgsoni*, *Oradarea edentata*, *E. georgiana* (one specimen) and *E. perdentatus* were added to our data set for comparative analysis.

The SIMPER (SIMilarity PERcentage–species contribution) routine in PRIMER was used to investigate the clusters found by both hierarchical cluster analysis and MDS.

Parametric tests were used to compare isotope ratios between different taxa. Normality of the data was checked by the Kolmogorov-Smirnov test followed by ANOVA and post-hoc (Tukey test) comparisons of means. A significance level of $p < 0.001$ was used in all tests (Scherrer 1984) except when it is mentioned.

3.3. RESULTS

3.3.1. STOMACH CONTENT & TROPHIC TYPE

Major stomach contents and corresponding trophic type of the 11 amphipod species are summarized in Table 3.1. Detailed stomach content data are provided by Dauby et al. (2001b) and Nyssen et al. (2002). Trophic type of the 11 species ranged from suspension feeder to scavenger.

Table 3.1. Classification of 11 species of Antarctic amphipods in different trophic categories following the composition of their stomach contents (Dauby et al. 2001b, Nyssen et al. 2002, this study)

Species	Trophic type	Major prey
<i>Ampelisca richardsoni</i>	Suspension feeder	Phytoplankton
<i>Djerboa furcipes</i>	Herbivore	Brown Macroalgae
<i>Epimeria similis</i>	Micropredator	Hydrozoan
<i>Epimeria georgiana</i>	Deposit feeder	Detritus
<i>Eusirus perdentatus</i>	Predator	Crustaceans
<i>Echiniphimedia hodgsoni</i>	Micro predator	Sponges
<i>Iphimediella</i> sp	Predator	Crustaceans
<i>Pseudorchomene coatsi</i>	Scavenger	Carrion
<i>Abyssorchomene plebs</i>	Scavenger	Carrion
<i>Eurythenes gryllus</i>	Scavenger	Carrion
<i>Waldeckia obesa</i>	Scavenger	Carrion

3.3.2. FATTY ACID COMPOSITION

The fatty acid composition, albeit different between species, showed some overall similarities (Table 3.2). The principal fatty acids of all species were 16:0, 18:1 (both isomers), 20:4(n-6), 20:5(n-3) and 22:6(n-3). High percentages of polyunsaturated fatty acids (PUFA) were found in *A. richardsoni* (58%) whereas monounsaturated fatty acids (MUFA) were most abundant in *E. gryllus*, accounting for up to 58%. The hierarchical cluster analysis separated twelve amphipod species into 5 distinct groups at the 80% similarity level (Fig. 3.2, see p.21). Clusters C1 and C5 are mono-specific and Cluster 4 is well separated into single species groupings. In Clusters C2 and C3 the individuals are not gathered by species in subgroups but more spread, although some separation was still apparent. *Iphimediella* sp. and one specimen of *E. hodgsoni* remained outside the clusters defined at the 80% similarity level: As shown by the SIMPER analysis (Table 3.3), these groupings had high, within group, similarities. The statistical treatment, using all fatty acids for each group indicated that essentially the oleic acid (18:1(n-9)) distinguished Cluster 1 (*W. obesa*) from all other clusters. The fatty acid profile of *W. obesa* was unique since oleic acid accounted for more than 44% of total fatty acids. This unusually high proportion of oleic acid is responsible for the split of scavenger species into two different clusters (C1 and C2). The SIMPER analysis revealed also that it is mainly the higher proportion of the fatty acid 18:4(n-3) which isolates Cluster 5 from the other Clusters. The highest levels of C₁₈ and C₂₀ PUFA (mainly arachidonic acid (20:4(n-6)), which is the discriminant fatty acid for this cluster) occurred in Cluster 4 (*D. furcipes* and *O. edentata*). Besides all the clusters, the isolated position of the iphimeriid species in the dendrogram seems to be due to its considerably high levels of 20:1 and 22:1 fatty acids (19% in total).

Table 3.2. Fatty acid composition (mean value \pm SD) of total lipid extracted from 12 species of amphipods from the Southern Ocean. Only values $\geq 0.3\%$ are mentioned. Number of analysed individuals in brackets. Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Eh—*Echiniphimedia hodgsoni*, Ep—*Eusirus perdentatus*, Df—*Djerboa furcipes*, Oe—*Oradarea edentata* (data from Graeve et al. (2001), Ar—*Ampelisca richardsoni*, Iphi—*Iphimediella* sp

Fatty acids	Wo (7)	Ap (9)	Eg (2)	Pc (1)	Es (2)	Ege (2)	Eh (2)	Ep (1)	Df (2)	Oe (2)	Ar (3)	Iphi (1)
14:0	11.3 \pm 2.9	3.4 \pm 1.0	1.7 \pm 0.9	6.9	1.3 \pm 0.1	1.1 \pm 0.1	0.7 \pm 0.1	2.1	1.0 \pm 0.1	1.6 \pm 0.1	5.3 \pm 0.2	3.5
15:0	0.8 \pm 0.9	0.3	0.2 \pm 0.1	0.4	1.2 \pm 0.4	0.9 \pm 0.4	0.7 \pm 0.1	0.4	0.6 \pm 0.1	0.6 \pm 0.2	0.1	0.4
16:0	12.9 \pm 1.6	12.9 \pm 2.0	11.0 \pm 2.9	22.5	13.4 \pm 3.5	11.4 \pm 1.9	8.9 \pm 1.1	15.3	16.8 \pm 1.1	14.7	8.8 \pm 0.6	12.5
17:0	0.4 \pm 0.3	0.9 \pm 0.8	0.1 \pm 0.1	0.2	0.5 \pm 0.1	0.3 \pm 0.3	0.1	0.1	2.0 \pm 2.8	0.1	0.1	0.4
18:0	1.9 \pm 0.8	1.1 \pm 0.3	1.8 \pm 0.2	2.9	1.1 \pm 0.1	1.1 \pm 0.5	1.1 \pm 0.1	0.9	1.7 \pm 0.1	0.5 \pm 0.1	1.2 \pm 0.2	3.0
16:1(n-7)	6.7 \pm 1.4	10.0 \pm 3.2	7.5 \pm 0.6	7.9	2.1 \pm 0.4	3.6 \pm 1.3	11.4 \pm 1.5	3.7	3.1 \pm 0.3	7.4 \pm 1.4	9.1 \pm 1.9	3.9
18:1(n-9)	44.1 \pm 2.7	30.5 \pm 4.9	33.9 \pm 2.7	31.1	20.2 \pm 1.6	21.9 \pm 0.2	19.9 \pm 5.2	22.7	17.7 \pm 1.1	20.9 \pm 0.7	8.3 \pm 0.7	19.7
18:1(n-7)	2.9 \pm 2.1	6.8 \pm 0.9	7.4 \pm 0.6	6.2	6.1 \pm 0.2	8.4 \pm 0.5	10.6 \pm 3.6	5.2	3.3 \pm 0.2	5.1 \pm 1.1	3.3	6.1
20:1(n-9)	1.1 \pm 0.5	5.1 \pm 2.9	4.9 \pm 0.3	2.6	1.9	1.8 \pm 0.7	1.1	1.3	1.0 \pm 1.3	1.6 \pm 0.1	1.4 \pm 0.2	9.3
20:1(-7)	0.3 \pm 0.1	0.9 \pm 0.3	1.9 \pm 0.7	0.5	1.0 \pm 0.7	2.3 \pm 0.4	2.8 \pm 0.9	0.7	0.0	0.3 \pm 0.3	0.6 \pm 0.1	5.8
22:1(n-11)	0.6 \pm 0.6	1.5 \pm 1.0	1.7 \pm 1.5	2.5	0.3 \pm 0.2	0.4 \pm 0.2	0.2 \pm 0.1	0.2	0.6 \pm 0.8	0.3 \pm 0.2	0.1	3.5
22:1(n-9)	0.1 \pm 0.1	0.6 \pm 0.7	0.5 \pm 0.6	0.1	0.5 \pm 0.4	0.4 \pm 0.1	0.7 \pm 0.4	0.4	0.0	0.3	0.1	0.1
16:2(n-4)	0.5 \pm 0.2	0.6 \pm 0.9	3.2 \pm 4.2	1.2	0.7 \pm 0.1	0.6 \pm 0.1	0.6 \pm 0.7	0.5	1.8 \pm 0.1	2.3 \pm 0.3	2.1 \pm 0.5	1.6
18:2(n-6)	1.0 \pm 0.3	1.8 \pm 0.3	1.8 \pm 0.4	1.1	1.7 \pm 0.1	1.8 \pm 0.3	4.7 \pm 2.2	2.2	5.4 \pm 0.4	3.6 \pm 0.2	2.0 \pm 0.2	1.2
16:3(n-4)	1.0 \pm 0.2	0.4 \pm 0.1	0.5 \pm 0.1	0.5	0.6 \pm 0.5	0.8 \pm 0.2	1.1 \pm 0.1	0.5	0.3 \pm 0.4	0.8 \pm 0.1	0.4 \pm 0.1	0.5

Fatty acids	Wo (7)	Ap (9)	Eg (2)	Pc (1)	Es (2)	Ege (2)	Eh (2)	Ep (1)	Df (2)	Oe (2)	Ar (3)	lphi (1)
16:4(n-1)	0.1	0.2 ±0.1	0.8 ±0.8	0.1	0.0	0.1	0.1	0.1	0.0	0.1	1.4 ±0.6	0.1
18:3(n-6)	0.2	0.2	0.5 ±0.1	0.1	0.2 ±0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.2
18:3(n-3)	0.2	0.5 ±0.1	0.5 ±0.2	0.4	0.5 ±0.2	0.5 ±0.3	0.8 ±0.2	0.8	3.3 ±0.5	2.7 ±0.3	1.2	0.3
18:4(n-3)	0.3 ±0.1	0.8 ±0.4	0.6 ±0.2	0.8	0.7 ±0.6	0.7 ±0.5	0.3 ±0.3	1.7	1.8 ±0.4	1.9 ±0.5	21.4	0.3
20:4(n-6)	1.3 ±0.5	1.4 ±1.7	1.4 ±0.4	1.1	8.0 ±3.3	8.2 ±2.7	2.7 ±1.2	2.8	15.0 ±0.9	20.0 ±1.5	0.7	1.4
20:4(n-3)	0.1	0.5 ±0.2	0.6 ±0.2	0.5	0.4 ±0.4	0.3 ±0.1	0.1	0.4	0.7 ±0.1	0.8 ±0.1	3.1 ±0.4	0.5
20:5(n-3)	6.1 ±1.5	9.1 ±2.4	8.7 ±2.5	4.3	19.0 ±1.6	19.2 ±2.0	16.7 ±3.2	19.7	19.9 ±1.3	12.4 ±0.5	19.2 ±0.6	14.6
22:5(n-3)	0.6 ±0.8	1.6 ±0.8	0.4 ±0.1	1.0	0.8 ±0.3	1.2 ±0.1	0.3 ±0.3	0.7	0.8	1.3 ±0.2	0.1	2.9
22:6(n-3)	6.0 ±1.0	8.9 ±2.1	8.8 ±1.7	5.4	18.1 ±2.6	13.2 ±0.3	14.9 ±11.3	17.7	2.7 ±0.3	0.9 ±0.1	10.5 ±0.8	8.3
sum PUFA	15.8 ±4.4	23.6 ±7.9	22.7 ±6.4	14.2	48.2 ±9.6	44.2 ±6.3	37.1 ±16.6	44.5	44.3 ±3.8	41.1 ±3.3	58.0 ±2.5	29.1
C18 ratio	15.0	4.5	4.6	5.0	3.3	2.6	1.9	4.3	5.4	4.1	2.5	3.3
sum 20:1	1.4 ±0.7	6.0 ±3.1	6.8 ±1.0	3.1	2.9 ±0.7	4.1 ±1.1	3.9 ±0.9	1.9	1.0 ±1.3	1.9 ±0.4	2.0 ±0.3	15.0
sum 22:1	0.7 ±0.7)	2.1	2.1 ±2.1	2.6	0.8 ±0.6	0.8 ±0.3	0.9 ±0.6	0.6	0.6 ±0.8	0.6 ±0.3	0.2	3.6

3.3.3. STABLE ISOTOPE RATIOS

The average carbon and nitrogen isotope ratios range from -29.3‰ ($\delta^{13}\text{C}$) and 4.1‰ ($\delta^{15}\text{N}$) in *A. richardsoni* to -21.7‰ ($\delta^{13}\text{C}$) and 11.9‰ ($\delta^{15}\text{N}$) in *Iphimediella* sp (Table 3.4). The inter-species differences are significant as indicated by ANOVA and subsequent post-hoc tests (Tables 3.5a & 3.5b). Displaying the lowest isotopic ratios, *A. richardsoni* ($\delta^{13}\text{C} = -27.1 \pm 0.9\text{‰}$; $\delta^{15}\text{N} = 6.6 \pm 0.6\text{‰}$) and *D. furcipes* ($\delta^{13}\text{C} = -23.4 \pm 0.6\text{‰}$; $\delta^{15}\text{N} = 4.9 \pm 0.3\text{‰}$) resemble primary producers, i.e. the suspended particulate organic matter and the brown macroalgae *Desmarestia mensiezii*. The isotopic ratios of these primary consumers are significantly different from values of all the other species (Tukey test, $p < 0.001$).

Both Epimeriidae and the species *E. perdentatus* show wide ranges of isotopic ratios. As illustrated in Figure 3.3 (see p.24), the range of values is wider for $\delta^{13}\text{C}$ than for the $\delta^{15}\text{N}$. The difference between maximum and minimum $\delta^{13}\text{C}$ is from 2.5 to 5.5‰. This difference is less pronounced for nitrogen (from 1.5 to 3‰). The species displaying the widest range of values is *E. georgiana*. The scavengers are clearly separated into two groups and this scission is essentially due to their significantly different $\delta^{13}\text{C}$ (Tukey test, $p < 0.001$). The first group is composed of the lipid-rich species *A. plebs* and *E. gryllus* while the second gathers the lipid-less *W. obesa* and *P. coatsi* (Nyssen & Graeve, unpublished results).

Table 3.4. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of 11 species of Antarctic amphipods (mean \pm SD); n: number of samples.

Species	N	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$
<i>Ampelisca richardsoni</i>	3	-29.3 ± 0.2	4.1 ± 0.1
<i>Djerboa furcipes</i>	5	-27.8 ± 0.6	4.9 ± 0.3
<i>Eusirus perdentatus</i>	14	-23.4 ± 0.6	7.3 ± 1.0
<i>Epimeria similis</i>	15	-25.0 ± 1.5	7.6 ± 0.5
<i>Epimeria georgiani</i>	17	-23.7 ± 1.7	7.9 ± 0.4
<i>Echiniphimedia hodgsoni</i>	2	-24.3 ± 1.3	10.6 ± 1.8
<i>Iphimediella</i> sp	4	-21.7 ± 1.2	11.9 ± 0.9
<i>Pseudorchomene coatsi</i>	3	-22.7 ± 0.3	9.3 ± 0.3
<i>Abyssorchomene plebs</i>	6	-26.6 ± 0.5	9.5 ± 0.8
<i>Eurythenes gryllus</i>	9	-27.3 ± 1.1	8.5 ± 0.5
<i>Waldeckia obesa</i>	5	-22.8 ± 0.9	7.3 ± 0.7

The highest positioned species in the food web, *Iphimediella* sp. displays significantly different $\delta^{15}\text{N}$ to the other species (Tukey test, $p < 0.001$) except from *E. hodgsoni* which belongs to the same family. However, the $\delta^{13}\text{C}$ value shows some similarity with other species, such as *W. obesa*, *E. perdentatus*, *P. coatsi* and *E. georgiana*.

Table 3.3. Results of SIMPER analysis: within-group similarity (% in parenthesis), average dissimilarity (%) and separating fatty acids (FA) (most discriminant).

Average Dissimilarity + separating FA	CLUSTER 1 (89.1%)	CLUSTER 2 (83.7%)	CLUSTER 3 (81.8%)	CLUSTER 4 (85.3%)	CLUSTER 5 (95.0%)
CLUSTER 1	-	25.4% 18:1(n-9)/14:0	41.1% 18:1(n-9)/20:5(n-3)	44.3% 18:1(n-9)/20:4(n-6)	50.5% 18:1(n-9)/18:4(n-3)
CLUSTER 2		-	29.7% 18:1(n-9)/20:5(n-3)	36.8% 20:4(n-6)/18:1(n-9)	43.2% 18:1(n-9)/18:4(n-3)
CLUSTER 3			-	29.9% 22:6(n-3)/20:4(n-6)	36.7% 18:4(n-3)/18:1(n-9)
CLUSTER 4				-	44.5% 18:4(n-3)/20:4(n-6)
CLUSTER 5					-

Table 3.5a. ANOVA results: post-hoc test (Tukey test) for $\delta^{13}\text{C}$. “x” indicates significant with $p < 0.001$, “x*” indicates significant with $p < 0.005$ and “ns” indicates no significant difference between means at $\alpha = 0.05$.

	Species	N	$\delta^{13}\text{C}$	1	2	3	4	5	6	7	8	9	10	11
1	<i>A. richardsoni</i>	3	-29.3 ± 0.2		ns	x	x	x	x	x	x*	ns	x	x
2	<i>D. furcipes</i>	5	-27.8 ± 0.6			x	x	x	x*	x	ns	ns	x	x
3	<i>E. similis</i>	15	-25.0 ± 1.5				x	x*	ns	x	ns	x	ns	x*
4	<i>E. georgiana</i>	17	-23.7 ± 1.7					ns	ns	ns	x	x	ns	ns
5	<i>E. perdentatus</i>	14	-23.4 ± 0.6						ns	ns	x	x	ns	x*
6	<i>E. hodgsoni</i>	2	-24.3 ± 1.3							ns	ns	x*	ns	ns
7	<i>Iphimediella</i> sp.	4	-21.7 ± 1.2								x	x	ns	ns
8	<i>A. plebs</i>	6	-26.6 ± 0.5									ns	x	x
9	<i>E. gryllus</i>	9	-27.3 ± 1.1										x	x
10	<i>P. coatsi</i>	3	-22.7 ± 0.3											ns
11	<i>W. obesa</i>	5	-22.8 ± 0.9											

Table 3.5b. ANOVA results: post-hoc test \pm Tukey test) for $\delta^{15}\text{N}$. “x” indicates significant with $p < 0.001$, “x*” indicates significant with $p < 0.005$ and “ns” indicates no significant difference between means at $\alpha = 0.05$, n: number of samples.

	Species	N	$\delta^{15}\text{N}$	1	2	3	4	5	6	7	8	9	10	11
1	<i>A. richardsoni</i>	3	4.1 ± 0.1		ns	x	x	x	x	x	x	x	x	x
2	<i>D. furcipes</i>	5	4.9 ± 0.3			x	x	x	x	x	x	x	x	x
3	<i>E. similis</i>	15	7.6 ± 0.5				ns	ns	x	x	ns	ns	ns	ns
4	<i>E. georgiana</i>	17	7.9 ± 0.4					x	ns	x	ns	ns	ns	ns
5	<i>E. perdentatus</i>	14	7.3 ± 1.0						x	x	x	ns	x	ns
6	<i>E. hodgsoni</i>	2	10.6 ± 1.8							ns	ns	ns	ns	x
7	<i>lphimediella</i> sp.	4	11.9 ± 0.9								x	x	x*	x
8	<i>A. plebs</i>	6	9.5 ± 0.8									ns	ns	x*
9	<i>E. gryllus</i>	9	8.5 ± 0.5										ns	ns
10	<i>P. coatsi</i>	3	9.3 ± 0.3											ns
11	<i>W. obesa</i>	5	7.3 ± 0.7											

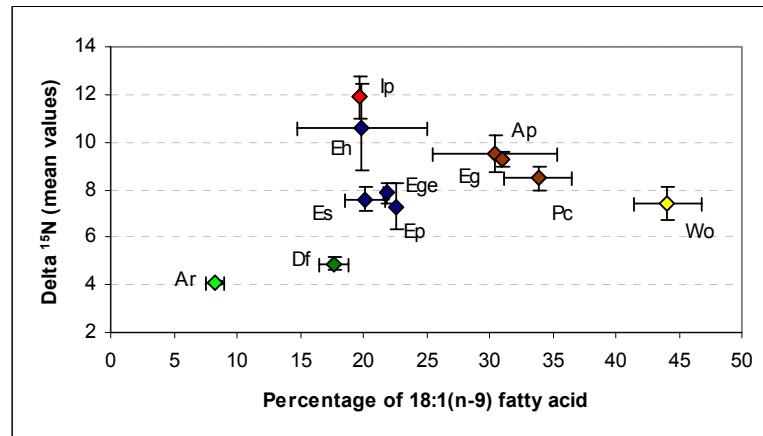
3.3.4. THE 2-DIMENSIONAL BIOMARKER APPROACH

In order to check whether the combination of fatty acid and stable isotope data is useful to enhance the identification of trophic positions, $\delta^{15}\text{N}$ values were plotted versus four fatty acid types which are characteristic biomarkers for certain food types or feeding strategies (Figs 3.4a to 3.4b).

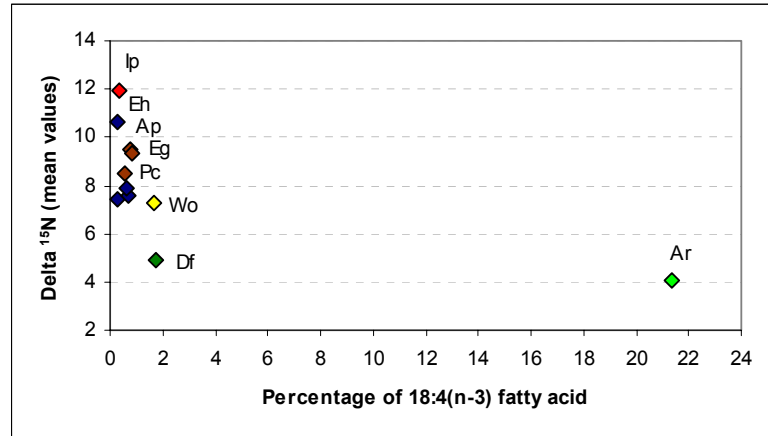
18:1(n-9) fatty acid is considered to be a signature of carnivory (Graeve et al. 2001, Auel et al. 2002). There is a general positive relationship between $\delta^{15}\text{N}$ and 18:1(n-9) (Fig 3.4a). The negative relationship between $\delta^{15}\text{N}$ and the polyunsaturated fatty acid 18:4(n-3), recognized as a biomarker of haptophytes (Graeve et al. 1994a, b), is illustrated in Figure 3.4b. The distinction between primary consumers food preferences is evident from comparison of Figures 3.4b and 3.4c. Finally, the plot of 20:1 and 22:1 fatty acids, synthesized only by calanoid copepods (Graeve et al. 1994a, b, Hagen et al. 1993, 2000, Kattner et al. 1994), against $\delta^{15}\text{N}$ shows a clear positive correlation (Fig. 3.4d).

Figs.3.4a to 3.4d. Nitrogen isotopic ratios plotted vs concentration of fatty acid biomarkers (% of total fatty acids) of 11 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Ep—*Eusirus perdentatus*, Ip—*Iphimediella* sp., Eh—*Echiniphimedia hodgsoni*, Ar—*Ampelisca richardsoni*, Df—*Djerboa furcipes*.

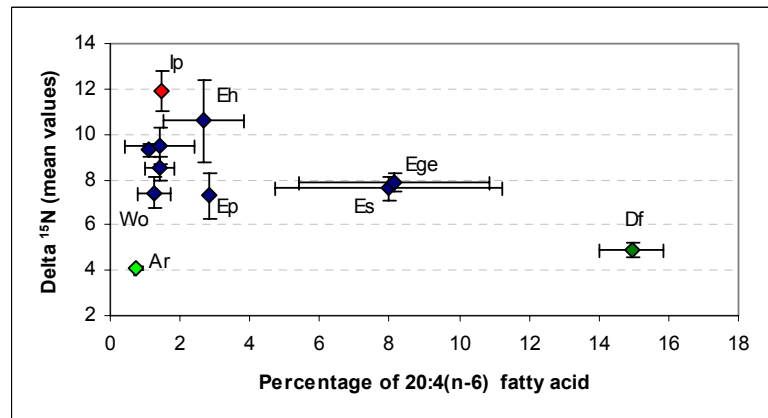
3.4a



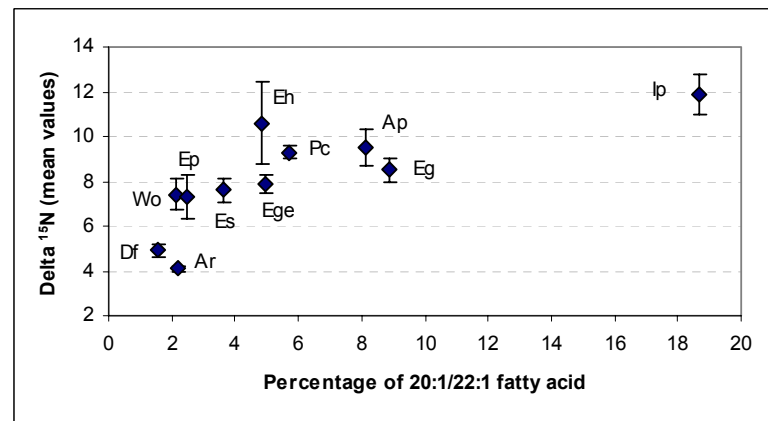
3.4b



3.4c



3.4d

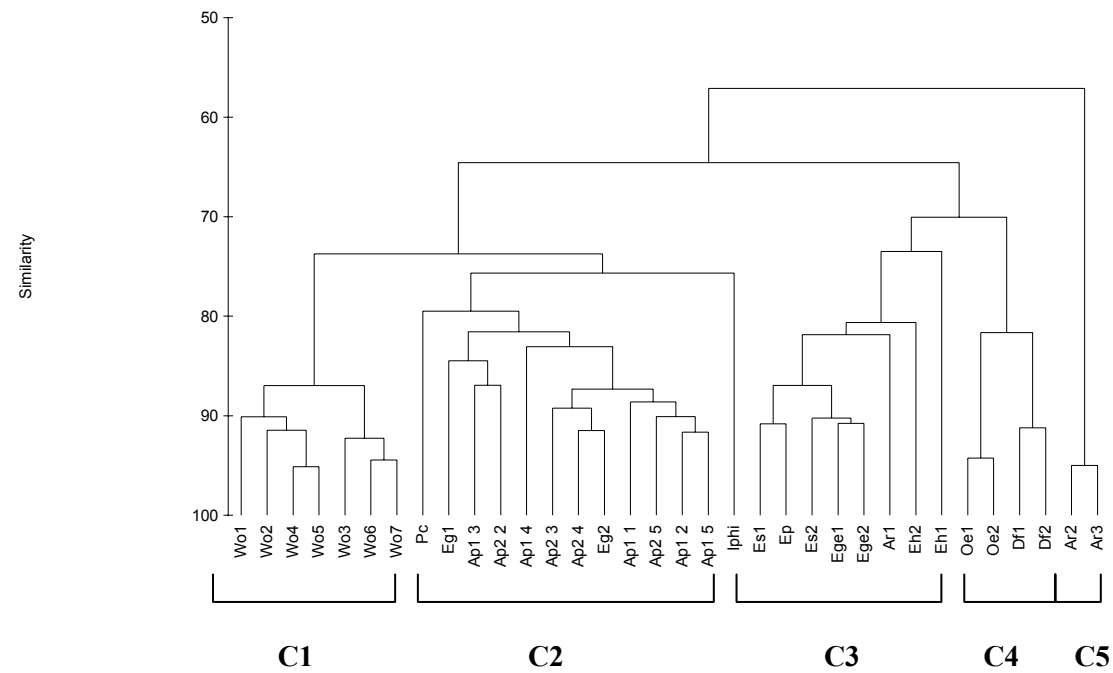


3.4. DISCUSSION

SIMPER analysis involving all fatty acids revealed essentially the oleic acid, to distinguish Cluster 1 from all other clusters. The fatty acid signature of *W. obesa* is characterized by extremely high levels of 18:1(n-9) and high levels of 14:0 compared to all other species. This unusual amount of 18:1(n-9) has already been recorded by Graeve et al. (2001) for the same species. Oleic acid is a major end product of the fatty acid biosynthesis in vertebrates and invertebrates. For example, Iverson et al. (2002) have reported concentrations of more than 30% of this fatty acid in Alaskan eulachon (*Thaleichthys pacificus*). In Antarctic waters, the notothenioid fishes, such as the icedevil, *Aethotaxis mitopteryx*, and the silverfish, *Pleurogramma antarcticum*, also display rather high levels of 18:1(n-9) fatty acid (about 25% of the total fatty acid composition) (Hagen et al. 2000) but none of them have ever been found to contain concentrations as high as those recorded in scavenging amphipods. The fatty acid 18:1(n-9), typically occurring in metazoans, is generally considered as a signature of carnivorous feeding (Sargent & Henderson 1986, Falk-Petersen et al. 1990, Graeve et al. 1994b, 1997, Hagen & Kattner 1998, Auel et al. 2002). Plotted against $\delta^{15}\text{N}$, which is a trophic indicator, a general positive correlation is observed, and an accumulation of 18:1(n-9) from the diet could be suggested. However, a particularly high *de novo* biosynthesis of 18:1(n-9) could also explain those high concentrations in Lysianassidae in general and *W. obesa* in particular. These fatty acids could have been synthesized by amphipods in response to short periods of satiety followed by long periods of starvation, a common situation for scavengers. Cluster 2, comprising the other scavengers, *A. plebs*, *E. gryllus* and *P. coatsi*, is also characterized by high levels of 18:1(n-9) but to a lesser extent compared to *W. obesa*. This difference, associated with the different levels of 14:0 fatty acid, is responsible for 40% of the separation of scavenger amphipods in two different clusters.

Considering the isotopic results, the species *A. plebs* and *E. gryllus* are characterized by particularly low $\delta^{13}\text{C}$ values compared to the other scavengers *W. obesa*, and *P. coatsi*. This depletion in carbon is probably due to the higher lipid content of *A. plebs* and *E. gryllus* (Nyssen & Graeve, unpublished results). Lipids are isotopically lighter than proteins and so high lipid content generally results in a decrease of the $\delta^{13}\text{C}$ of the whole body (DeNiro & Epstein 1977, Tieszen et al. 1983, Wada et al. 1987, Pinnegar & Polunin 1999, Nyssen et al. 2002).

Fig 3.2. Hierarchical cluster analysis of fatty acid composition (%) of the total lipid extracted from 12 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Eh—*Echiniphimedia hodgsoni*, Ep—*Eusirus perdentatus*, Df—*Djerboa furcipes*, Oe—*Oradarea edentata* (data from Graeve et al. (2001)), Ar—*Ampelisca richardsoni*, Iphi—*Iphimediella* sp.



All these scavenging amphipods belong to the family of the Lysianassidae and the conservation of a similar fatty acid composition in all of these congeners is particularly striking. A potential link between phylogeny and fatty acid composition in Lysianassids would be an interesting topic in itself. Indeed, the fatty acid composition of another Antarctic scavenger, the isopod *Natatolana* sp., is distinctly different despite its almost identical feeding strategy and prey spectrum (Nyssen, unpublished data).

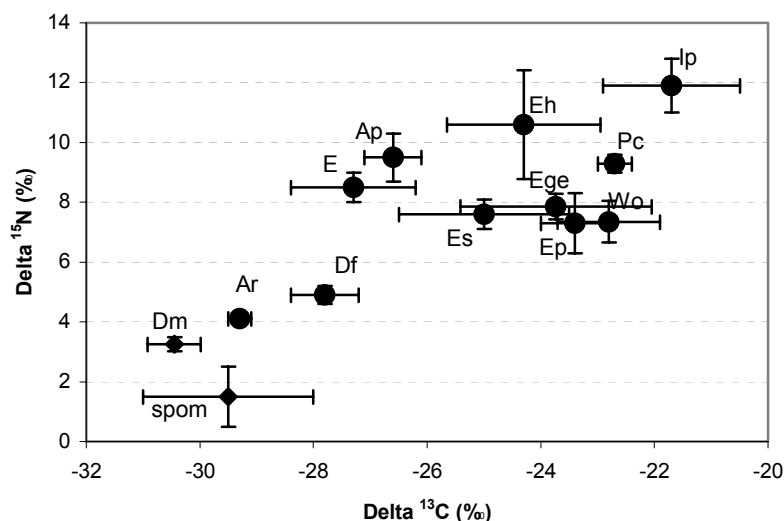
The high levels of C₁₈ and C₂₀ PUFAs (mainly arachidonic acid 20:4(n-6)) recorded in *D. furcipes* and *O. edentata* (Cluster 4, Fig 3.2) are well in accordance with their herbivorous diet. High concentrations of C₁₈ and C₂₀ polyunsaturated fatty acids have been shown to be typical of many macroalgae (Kayama et al. 1989, Cook et al. 2000, Graeve et al. 2001, Kharlamenko et al. 2001). Furthermore, judging by stomach content results, the brown alga *Desmarestia menziesii* seems to be preferentially consumed by these herbivorous amphipods. The results are corroborated by the fatty acid composition of the macroalgae, which are dominated by 20:4(n-6), 18:1(n-9) and C₁₈ PUFAs (Nyssen, unpublished results). When plotted against the $\delta^{15}\text{N}$ of all species, the percentage of 20:4(n-6) displays a negative correlation; its concentration increases with decreasing ranking of the various species in the food web (Fig. 3.4c). Although they are not macroherbivore, both Epimeriidae species accumulate significant quantities of 20:4(n-6) with up to 8%. Although Graeve et al. (2002) suggested arachidonic acid as indicating a macroalgal origin; other authors have suspected protists in the sediment to be one of the sources of 20:4(n-6) (Bell & Sargent 1985, Fullarton et al. 1995, Howell et al. 2003). The presence of sediment in the stomach of *E. similis* and *E. georgiana* has already suggested at least a partial deposit feeding behaviour and 20:4(n-6) levels could reflect some assimilation of the sediment-associated micro-organisms. Furthermore, even with a significant amount of arachidonic acid, the intermediate nitrogen ratios of both Epimeriidae provide additional evidence of the distance to this fatty acid signature source. These species do probably not belong to a well-defined

trophic category but are able to modulate their feeding behaviour in response to food availability. The combination of the different approaches used here enables the classification of those epimeriid species into the wrong trophic category to be avoided. This omnivory is corroborated by the wide range of their $\delta^{13}\text{C}$ which could reflect the large spectrum of organic matter sources upon which they can rely.

The SIMPER analysis also revealed that it is mainly the higher concentration of 18:4(n-3) fatty acid which isolates *A. richardsoni* from the other amphipods. These levels attest to a major dietary input of material originating from phytoplankton such as cryptophytes and/or haptophytes (Harrington et al. 1970, Nichols et al. 1991, Graeve 1993, Graeve et al. 1994a, b, Swadling et al. 2000, Graeve et al. 2001). Figure 3.4b clearly illustrates the drastic decrease of $\delta^{15}\text{N}$, indicator of the trophic position, along with the increase of the proportions of 18:4(n-3), a biomarker for the assimilation of fatty acid of phytoplankton origin (Harrington et al. 1970, Nichols et al. 1991, Graeve 1993, Graeve et al. 1994a, b, Swadling et al. 2000, Graeve et al. 2001). In this case, confusion would have been caused by the use of stable isotopes alone to determine trophic links. If the $\delta^{15}\text{N}$ values indicate *A. richardsoni* and *D. furcipes* as primary consumers, their respective fatty acid profiles reveal that they do not rely on the same primary producers at all.

The rather isolated position of *Iphimediella* sp. (Fig.3.2) seems to be due to the significant proportions of both isomers of the long-chain monounsaturated 20:1 and 22:1 fatty acids. These long-chain monounsaturates are typical components of dominant Antarctic copepod species *Calanoides acutus* and *Calanus propinquus* (Hagen et al. 1993, Kattner et al. 1994, Hagen et al. 2000). The significance of these copepod biomarkers in the fatty acid pattern would put *Iphimediella* sp. in the zooplankton feeder group. However, its $\delta^{15}\text{N}$ value (highest value in Fig.3.4d) as well as its known predatory behaviour strongly indicates that there exists a trophic level between copepods and *Iphimediella* sp.

Fig.3.3. Carbon and Nitrogen isotopic ratios of 11 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Ep—*Eusirus perdentatus*, Ip—*Iphimediella* sp., Eh—*Echiniphimedia hodgsoni*, Ar—*Ampelisca richardsoni*, Df—*Djerboa furcipes*, spom—suspended particulate organic matter (data from Nyssen *et al.* 2002), Dm—brown macroalgae *Desmarestia mensezii*.



As illustrated in Figure 3.3 where $\delta^{15}\text{N}$ is plotted against $\delta^{13}\text{C}$, the other iphimiidiid species, *E. hodgsoni*, topped the trophic food web together with *Iphimediella* sp. With a diet essentially composed of sponges (Dauby *et al.* 2001b, Nyssen unpublished results), the high trophic position of *E. hodgsoni* is unexpected. Stable isotope ratios of Antarctic sponges can be quite high (-22.3 and 12.5 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively (Nyssen *et al.* 2002). This may be due to assimilation of rapidly sedimenting and isotopically heavy aggregates of sea ice origin (Dunton 2001) or to assimilation of resuspended matter that was cycled repeatedly through the microbial loop (Hobson *et al.* 1995, Nyssen *et al.* 2002 and references therein). The fatty acid profile of *E. hodgsoni* did not show any sign of particular reliance on special food items. Its profile is dominated by 20:5(n-3) and 22:6(n-3) which are typical for marine organisms and predominant

in membrane lipids (Sargent & Whittle 1981, Sargent & Henderson 1986, Albers et al. 1996, Graeve et al. 2001).

In conclusion, our study demonstrates that both fatty acid composition and stable isotope ratios are suitable tools for trophic ecosystem analysis in their own right. Fatty acids point towards food web links and stable isotopes identify trophic positions. However, the use of only one of the two tools can lead to misinterpretations with serious implications. The combination of the two approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution.

Acknowledgements

We would like to thank Profs A. Brandt (Hamburg) and W. Arntz (AWI, Bremerhaven) for their invitation to participate in the cruises ANDEEP and LAMPOS. We are also grateful to the officers and crew of the R.V. *Polarstern*, as well as to colleagues of the IRSNB (Brussels, Belgium) and AWI (Bremerhaven, Germany), who helped in collecting and sorting samples. The first author received a grant from the Belgian "Fonds de la Recherche pour l'Industrie et l'Agriculture" (FRIA). The present research was performed under the auspices of the Scientific Research Programme on Antarctic (Phase V) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs (contract no. EV/36/24A).

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CHAPTER 4: ANTARCTIC AMPHIPODS FEEDING HABITS INFERRED BY GUT CONTENTS AND MANDIBLE MORPHOLOGY

To be submitted

ABSTRACT

In this work, we have investigated the possibility to infer amphipod feeding type from morphology of amphipod mandible combined to the gut content composition. Ten species mouthparts have been dissected and examined with scanning electron microscopy (SEM). From gut content composition, four main trophic categories were distinguished: (micro- and macro-) herbivores, opportunistic predator, specialist carnivore and opportunistic scavenger. Macro-herbivores (*Djerboa furcipes*, *Oradarea* n. sp., *Oradarea walkeri*) show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The suspension-feeder (*Ampelisca richardsoni*) shows few molar ridges and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae. The opportunistic predator (*Eusirus perdentatus*) shows mandible morphology close to the basic model excepted for the molar which is tall, narrow and topped by a reduced triturative area. This could facilitate a fast ingestion. The species revealed as specialised carnivores (*Epimeria similis* and *Iphimediella cyclogena*) have been compared with other Antarctic species which also feed exclusively on the same item and the mandible morphology presented numerous dissimilarities. Finally, the molar development of scavenger species (*Tryphosella murrayi* and *Parschisturella carinata*) suggests that these animals rely on a broader dietary regime than carrion only. In any case, the smooth and sharp incisor of these lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

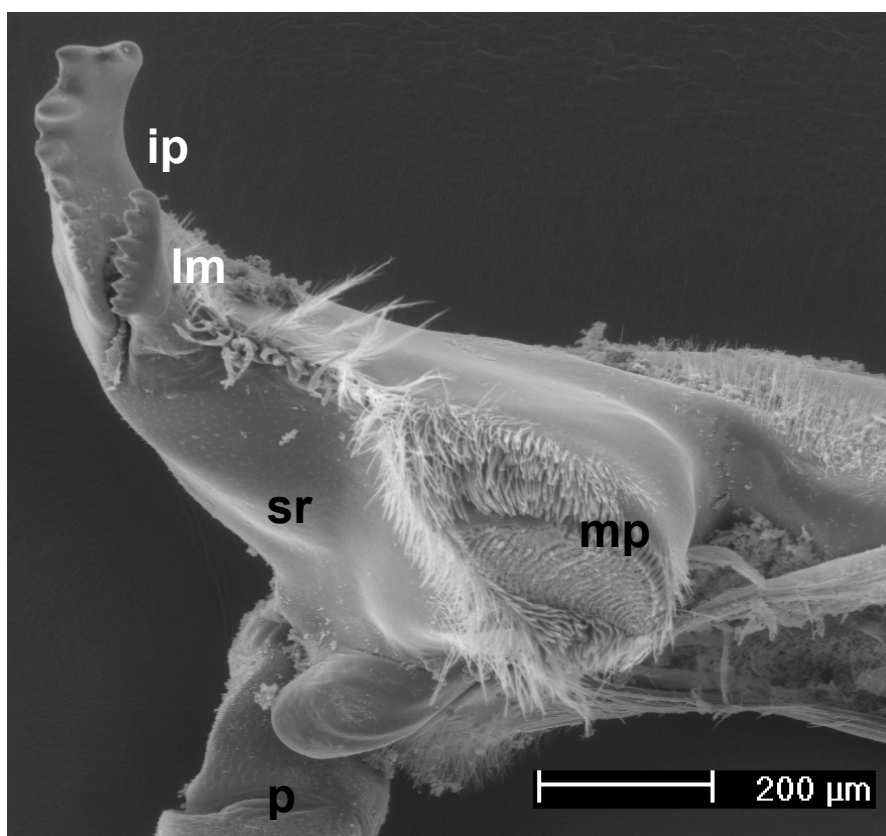
Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

4.1. INTRODUCTION

Despite a relatively low biomass Amphipoda constitute a significant group in terms of energy flux in the Antarctic shelf ecosystems (Jarre-Teichmann et al. 1997, Dauby et al. 2001b). Among Antarctic zoobenthos, these crustaceans represent one of the most speciose groups and probably the most diversified with respect to lifestyles, trophic types, habitats and size spectra (De Broyer & Jazdzewski 1996, Dauby et al. 2001a, Chapelle & Peck 1999, Nyssen et al. 2002). The ecofunctional and specifically the trophic role of those Antarctic amphipods is still poorly known. Constant and predictable environmental conditions as well as the high diversity (Knox and Lowry 1977) lead to an expectation of close niche adaptation and consequently the presence of many specialists to exploit the full spectrum of resources. The highly specialized mouthparts of many Antarctic amphipods widely illustrated by Coleman's work on Iphimediidae (1989a, b, c, 1990a, b) support the hypothesis of close niche adaptation to a preferred food source. The structure of the mandibles in particular has been sometimes interpreted as an adaptation to the presumed food source (Watling 1993).

The structure and function of crustacean mandibles have extensively been described by Manton in 1977. The basic gammaridean amphipod mandible is of the type observed in the genus *Gammarus* and most other gammaridean families (Barnard 1969). This basic morphology consists of a mandible body where four main structures are typically to be found, starting distally and going to the mouth opening: the **incisor process**, generally provided with cusps and teeth; the *lacinia mobilis*, inserted close to the incisor and generally in line with; the **spine-row**, filling the space between incisor and molar and probably involved in the transfer of the food to the mouth opening by forming a kind of bridge; and the **molar process**, a plane surface provided with diverse tritulative structures (Watling 1993).

Figure 4.1. mandible basic morphology (*Oradarea* n. sp. left mandible). ip: incisor process, mp: molar process, lm: *lacinia mobilis*, p: mandibular palp, sr: spine row.



A large panel of modifications to the basic pattern can be observed among peracarids. In his review of the functional morphology of the amphipod mandible, Watling (1993) divided the larger amphipod families into four groups in function of the degree of the modification of their mandible from the basic plan. As modifications, reduction of the incisor process, disappearance of the spine-row, reduction or complete loss of the molar process are observed in the different families. Most of those morphological changes appear as evolutionary patterns resulting from different feeding strategies as predation and/or scavenging feeding behavior. Several species of Iphimediidae and Lysianassoidea are good illustrations of some of those morphological adaptations (Dahl 1979, Sainte-Marie 1984, Coleman 1989b, c, 1990b, 1991, Watling 1993).

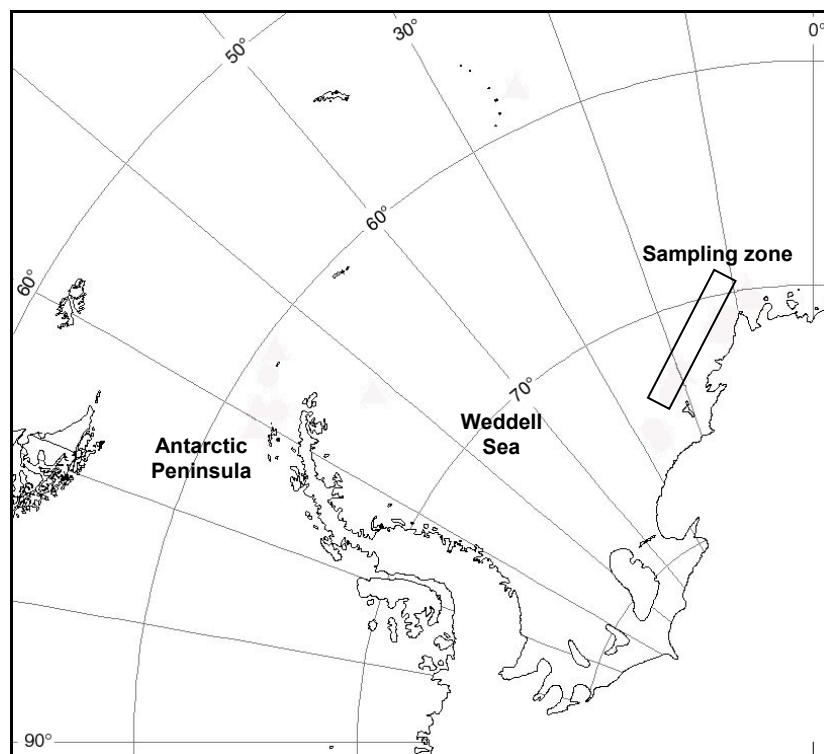
As a part of a multidisciplinary study of the amphipod ecological roles in Antarctic benthic systems (De Broyer et al. 2002), amphipod trophic patterns have been investigated (Dauby et al. 2001a, Graeve et al. 2001, Nyssen et al. 2002, De Broyer et al. 2004). The mandible morphology of ten species of Antarctic gammaridean amphipods has been studied and combined to gut contents analyses in an attempt to correlate mandible structure and feeding strategies.

4.2. MATERIAL AND METHODS

4.2.1. SAMPLING AND STORAGE

Amphipods (except three species) were collected from benthic and suprabenthic samples taken in the eastern Weddell Sea during three Antarctic summer cruises of RV “Polarstern”: EPOS leg 3 (1989; Arntz et al. 1990; De Broyer & Klages 1990), EASIZ I (1996; Arntz & Gutt 1997; De Broyer et al. 1997) and EASIZ II (1998; Arntz & Gutt 1999; De Broyer et al. 1999). Gears used included Agassiz, benthopelagic and bottom trawls, dredges and baited traps (Fig 4.2).

Fig.4.2. Map displaying sampling zone (rectangle) in the Eastern Weddell Sea



Catches of *Oradarea* n. sp., *Oradarea walkeri* and *Djerboa furcipes* were achieved in the upper part of the infralittoral of Admiralty Bay (King George Island, South Shetland Islands, Antarctic Peninsula) during spring tides and also by dredging in shallow water in the vicinity of the Polish base “Henryk Arctowski” during the summer season 1993 (Fig 4.3). All sampled species are listed in Table 4.1.

Fig.4.3. Map of Admiralty Bay, King George Island, Antarctic Peninsula

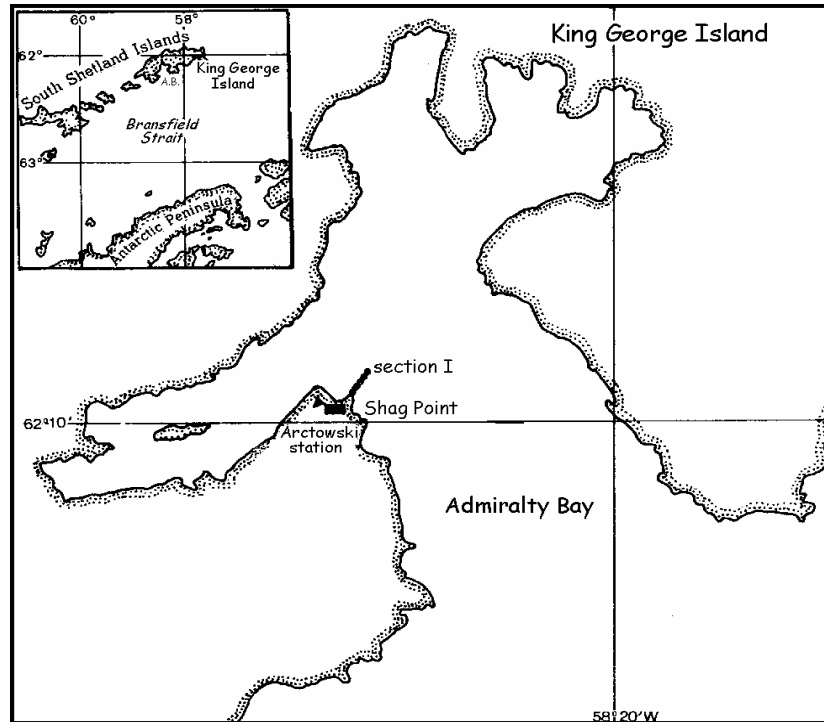


Table 4.1. List of sampled species, sampling sites and years, sex, size and feeding types

Family	Species	sampling	Site	Sex / size	Feeding type
Ampeliscidae	<i>Ampelisca richardsoni</i>	1998	E. Weddell Sea	Fem / 22mm	Suspension feeder
Eusiridae	<i>Oradarea</i> n. sp.	1994	S. Shetlands	Fem / 25mm	Herbivorous
Eusiridae	<i>Oradarea walkeri</i>	1993	S. Shetlands	Fem / 19mm	Herbivorous
Eusiridae	<i>Djerboa furcipes</i>	1993	S. Shetlands	Fem / 19mm	Herbivorous
Eusiridae	<i>Eurirus perdentatus</i>	1998	E. Weddell Sea	Fem / 38mm	Predator
Iphimediidae	<i>Iphimediella cyclogena</i>	1998	E. Weddell Sea	Fem / 35mm	Micro-predator
Epimeriidae	<i>Epimeria similis</i>	1996	E. Weddell Sea	Fem / 36mm	Micro-grazer
Epimeriidae	<i>Epimeria georgiana</i>	1998	E. Weddell Sea	Male / 26mm	Deposit feeder
Lysianassidae	<i>Parschisturella carinata</i>	1998	E. Weddell Sea	Fem / 20mm	Opport. scavenger
Lysianassidae	<i>Tryphosella murrayi</i>	1996	E. Weddell Sea	Fem / 25mm	Opport. scavenger

4.2.2. GUT CONTENT ANALYSIS

Analyses of gut contents were performed on 20 specimens from each species preserved in 4% formalin solution. Macroscopic dissections were conducted under a binocular dissecting microscope (Leica MZ12), using forceps and scissors. The digestive tract was cut at the oesophagus level and removed together with the midgut glands. Afterwards, it was separated from the midgut glands, opened and the content was spread on a micro slide. All the surface of the slide has been examined under optical microscope Leica DMLB (equipped with reflection contrast system). Every item has been identified as precisely as possible. The optic system was equipped with a video camera (JVC KY-F50) connected to a computer and pictures of the different food items were taken.

For several species, the gut contents results have been completed by Dauby *et al.* (2001a) wherein the methodological details can be found.

4.2.3. MORPHOLOGICAL ANALYSIS

Each species mouthparts were dissected (maxillipeds, maxillae 1 and 2, mandibles, upper and lower lips). Afterwards structures were dehydrated through an alcohol series, critical point dried and sputter-coated with carbon then gold to be observed with scanning electron microscopy (SEM). In this study, only the morphology of mandibles has been considered.

4.3. Results

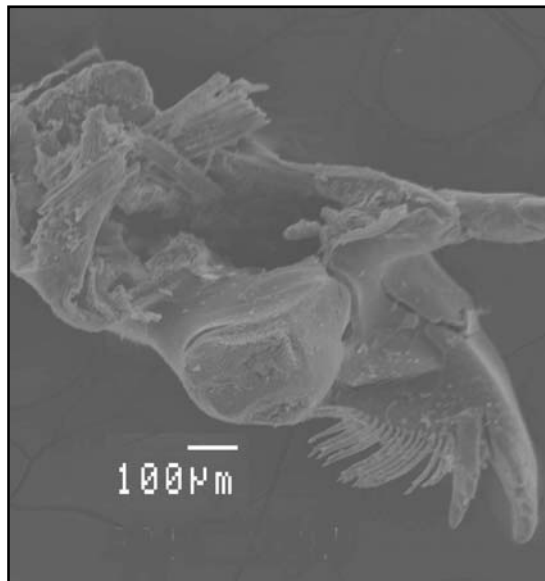
Ampelisca richardsoni Karaman, 1975 (suspension feeder)



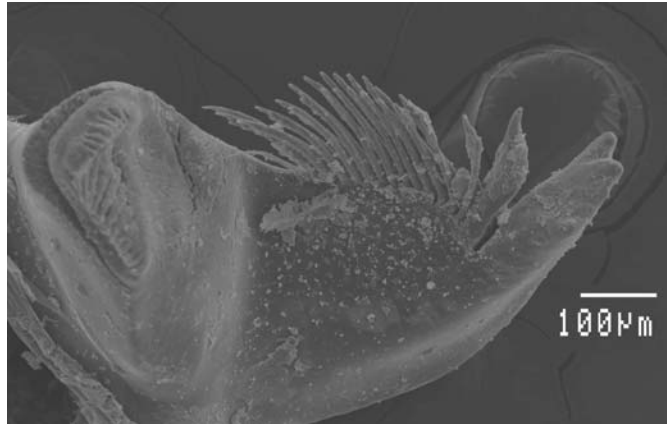
Examination of foregut and gut contents (see Dauby et al. 2001a). Food consists essentially of planktonic items (mainly diatoms) embedded in unidentified organic material (see picture on the left).

Mandible morphology.

Both mandibles bear well developed incisor and molar processes. Both incisors bear 5 rounded cusps but, whereas the left one (see picture on the right) is equipped by a strong 5-toothed *lacinia mobilis*.

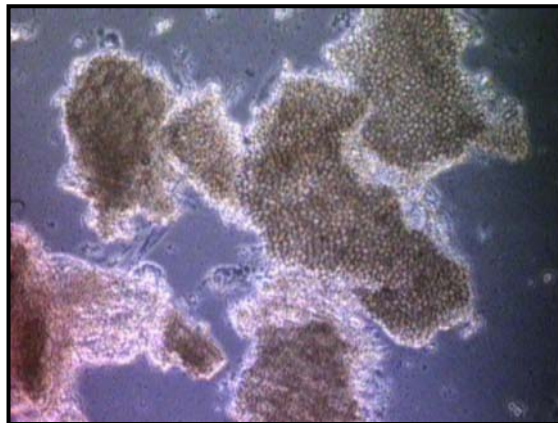


The right *lacinia mobilis* is smaller and more spine-like (see picture below). The molars are prominent and some smooth ridges are visible. The most striking feature of those mandibles is the development of the spine rows: on both side the row is composed of about 15 serrate spines nearly as long as the *lacinia mobilis* which could, by joining each other, form a kind of bridge between the tip of the mouthparts and the mouth itself.



Oradarea n. sp. (macroherbivore)

Examination of foregut and gut contents. The foregut and gut of 20 adult animals (female and ovigerous females) were examined. Those specimens were sampled by traps (400 meters depth) baited with different macroalgae (*Desmarestia menziesii* and *Iridea* sp.) and following the present algae species, gut composition



were totally different.

When baits consisted of pieces of the brown algae *D. menziesii*, 95% of the gut volume was filled with fragments of this algae

(see picture on the left, magnification X20).

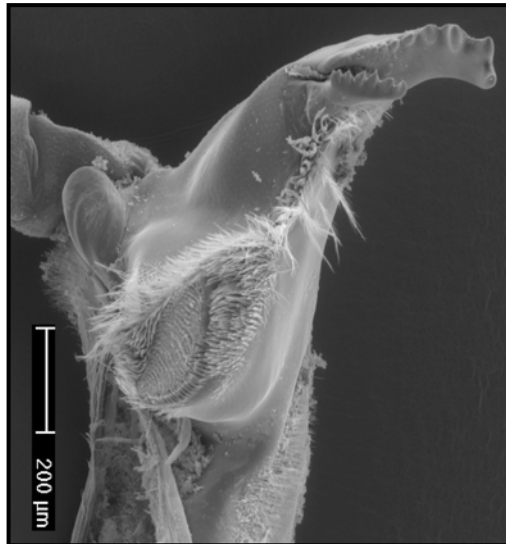


When baits consisted of pieces of algae belonging to the genus *Iridea*, (see picture on the left, magnification X80) the gut content was composed of: mineral particles, frustules of different

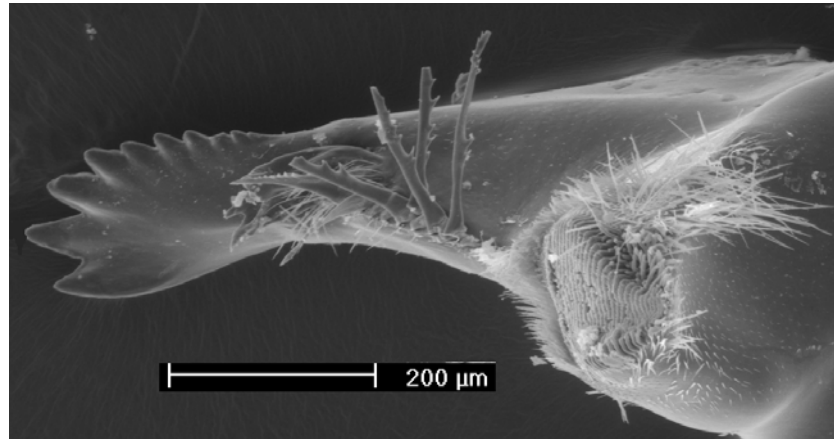
kind of diatoms, chitinous structures and in some specimens, a very few amount of pieces of the macroalgae *Iridea* sp.

Mandible morphology.

The mandibles are asymmetrical, although differing only in morphology of the *lacinia mobilis*. Incisor bears 10 rounded cusps. The left *lacinia* (see picture on the right) is similar to incisor although reduced in size and with only 7 more acute cusps.

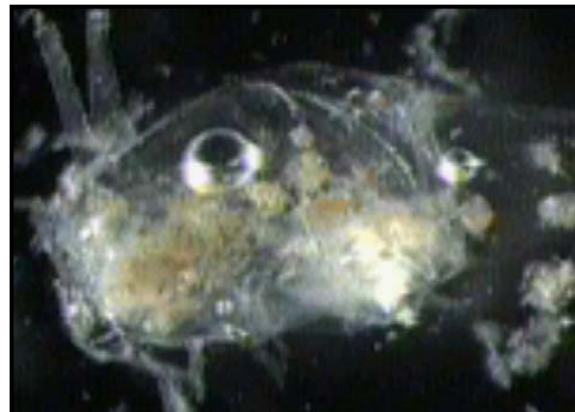


The right *lacinia* (see picture below) is slender. The spine row consists of stout serrate spines plus on the left mandible only a parallel row of plumose slender setae. The molar process is massive, sub columnar, and the tritritative area is closely surrounded by short and thick setae and topped by a dense crown of setae. The grinding surface is provided with densely set short spinules and ridges with serrate distal margin.

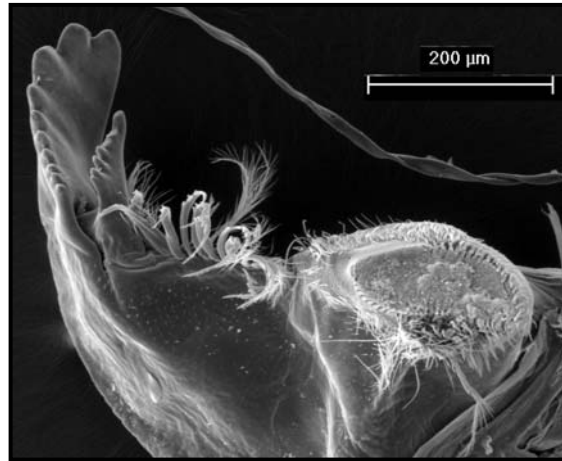


***Oradarea walkeri* Shoemaker, 1930 (macroherbivore)**

Examination of foregut and gut contents. 20 adult sampled by trawls (20-35m depth) were dissected. According to observation, 90% of gut contents were composed of pieces of macroalgae. The 10% left consisted of diatoms of



different types and inorganic material. The picture on the left represents the stomach of *O. walkeri* where pieces of macroalgae can be distinguished (green parts).



Mandible morphology.

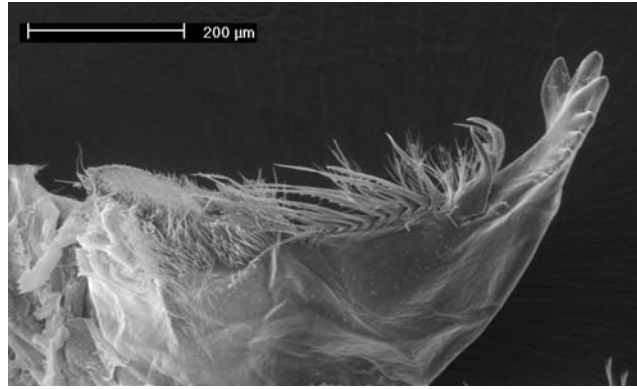
The morphology is nearly identical to that of *O. n.sp.* (see left mandible on the picture on the left). Both incisors are well developed and bear 10 strong teeth. The rather flat *corpus mandibulae*

is bordered ventrally by a double row of stout serrate setae and of slender plumose setae. The large and tall molars are topped by a dense fringe of setae and bear a large trituration area provided with ridges and other rasp-like structures. Both mandibles are flanked with a *lacinia mobilis*, strong and toothed (7 teeth) on the left mandible and weaker and spine-like on the right mandible.

***Dierboa furcipes* Chevreux, 1906 (macroherbivore)**

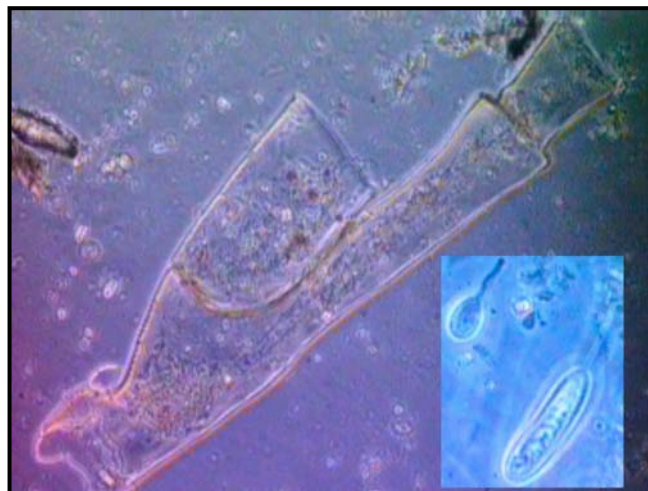
Examination of foregut and gut contents. Examination of the gut contents of 20 animals collected by trawls (20-35 m depth) allowed distinguishing – from the most to the less abundant item – : pieces of macroalgae thalli, pennate diatoms and a small amount of chitinous parts. All dissected specimens had also a significant amount of mineral particles in their gut.

Mandible morphology. As both species of the genus *Oradarea*, *D. furcipes* displays basic amphipod mandibles (in the sense of Watling 1993); toothed incisor (10 teeth), left *lacinia mobilis* with 10 teeth, only three on the right one (next page on top, see right mandible); large molar (but smaller than in genus *Oradarea*), cylindrical and trituration, crowned by a dense fringe of small setae; spine-row composed of two sort of setae.

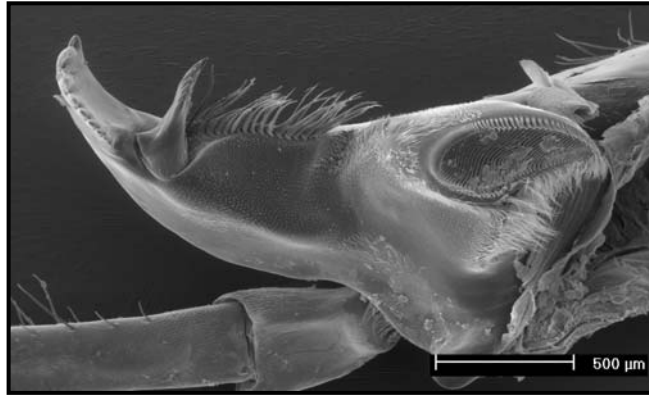


***Epimeria similis* Chevreux, 1912 (micropredator)**

Examination of foregut and gut contents. The gut content of *Epimeria similis* was dominated by hydroid perisarc fragments (see picture below) and cnidocysts of different shape and size (see small insert). The rest of the gut consisted of sponge spicules, microalgae (mainly centric diatoms and fragments of *Chaetoceros* sp.) and pieces of polychaetes.

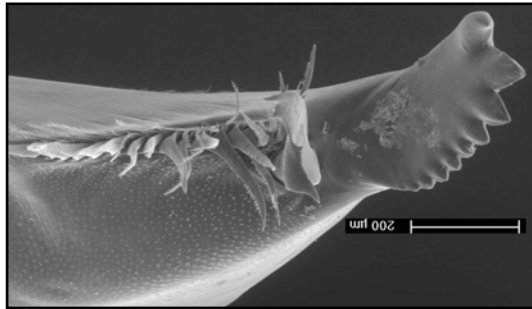


Mandible morphology. Both mandibles bear strong ten-toothed incisor and tall sub columnar molar provided with well-developed and smooth ridges.



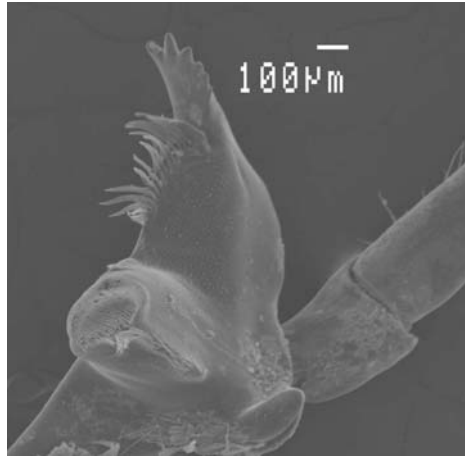
The molar is surrounded by a row of stubby setae and fringed with bundles of hairs at dorsal margin.

The left *lacinia mobilis* is armed with 7 cusps (see left mandible on the picture above) whereas the right one is smaller, bifurcated and spine-like (see the right mandible on the opposite picture). The spine-row is composed by stout denticulate setae, flanked on the ventral side by slender setae.



***Epimeria georgiana* Schellenberg, 1931 (deposit feeder)**

Examination of foregut and gut contents. The gut content of *E. georgiana* revealed a wide variety of food items: parts of crustaceans (mysids and amphipods), polychaetes, holothurian ossicles and hydrozoan perisarc and planktonic items as diatoms, radiolarians and foraminifers. Sponge spicules and mineral particles complete the food (see Dauby et al. 2001).

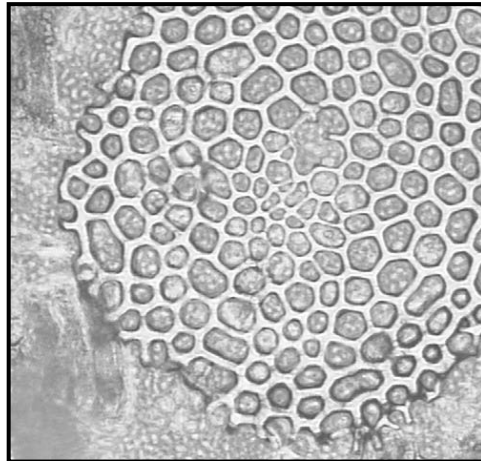


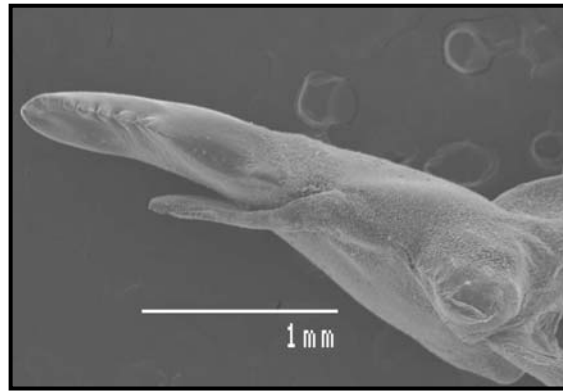
Mandible morphology. Both mandibles bear strong six-toothed incisor and as currently observed in this genus, the molars are prominent and provided with well developed ridges. The triturative area of molar is surrounded by a row of stubby setae and topped backward by bundles of hairs.

The left *lacinia mobilis* is toothed (5 cusps) whereas the right one is smaller and narrower (see right mandible on the picture above). The spine-row is composed by thick denticulate setae.

***Iphimediella cyclogena* K.H. Barnard, 1930 (micropredator)**

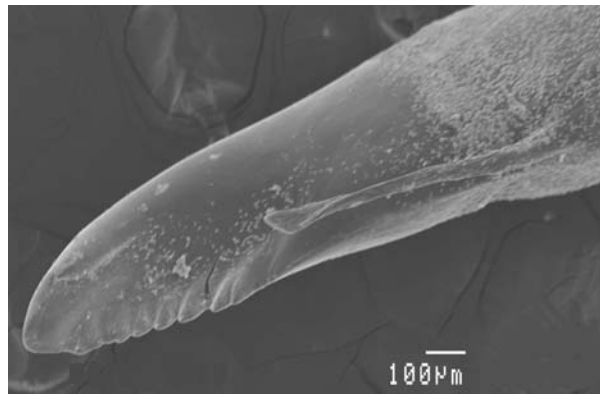
Examination of foregut and gut contents. The main food items observed in *I. cyclogena* gut were holothurian ossicles (see picture below) and polychaetes remains. In regard to the size of holothurians, it is more probable that this species scavenges instead of actually preying on it. *Iphimediella cyclogena* is considered as an opportunist consumer switching from predation to scavenging following the availability of food.





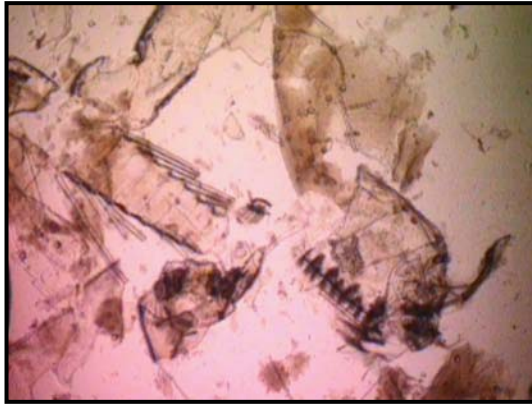
Mandible morphology.
(see left mandible on picture on the left).
The mandibular body is elongate tapering into the incisor that is much narrower than in all other species considered in this

work. Both incisor processes are toothed (10 cusps) and bear a long *lacinia mobilis* which is inserted near a molar process reduced to a small fleshy cone. The *lacinia mobilis* is thick and strongly chitinised on the left mandible and reduced to a thinner twiggy structure on the right mandible (see right mandible on picture below).



A major modification is the change in the orientation of the incisor, cutting in the vertical front plane. The position of the teeth along the incisor suggests a cutting in a scissor-like fashion.

Eusirus perdentatus Chevreux, 1912 (predator)



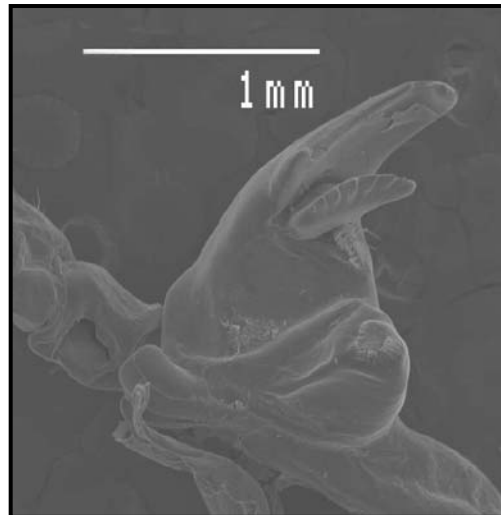
Examination of foregut and gut contents.

Crustacean hard parts and pieces of polychaetes form more than 50 percent of the gut contents (see picture on the left). Other food items consist of diatoms,

sponge spicules and inorganic material. These observations corroborated the conclusion of Klages & Gutt (1990) which said that *E. perdentatus* was a passive predator mainly feeding on crustaceans and polychaetes.

Mandible morphology. Mandibles bear strong incisors and molar processes.

On the left mandible the large *pars incisiva* bears dorsal and ventral cusps and is flanked with a denticulated (7 teeth) *lacinia mobilis* (see picture on the right). The right *lacinia mobilis* is armed with two teeth. The short spine-row is composed of about 10 spines.





The apex of the tall sub columnar molar bears a small tritulative area provided with rasp-like structures (see picture on the left). The reduced crushing area could explain the non-chewed state of some food items.

***Tryphosella murrayi* (Walker, 1903) (opportunistic necrophage)**

Examination of foregut and gut contents. Different items were observed in the digestive tract: pieces of crustaceans (antennae, buccal appendages, feathered setae, pleopods and ommatidia), pieces of polychaetes, very frequent fragments of flesh without any structure and some sponge spicules. The picture on the right presents a mid-gut full of fish flesh, parts of digestive caeca are also visible.





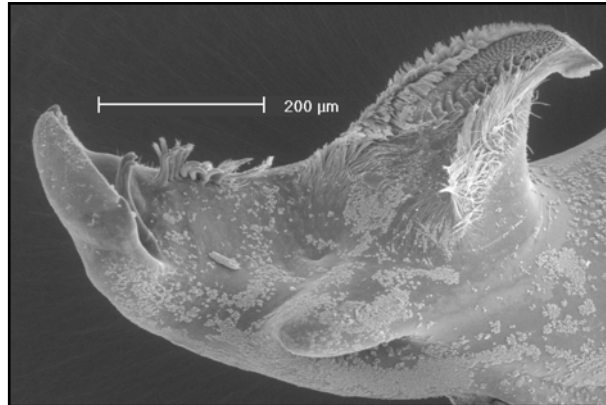
Mandible morphology. The proximal part of the incisors is narrow and the structure is broadening distally. The cutting edge is smooth and bears dorsal and ventral cusps. The *lacinia mobilis* is present on both mandibles. The spine-row is composed of 3 spines followed by a dense string of hairy setae which borders the corpus mandibulae. The molar is oval shaped and surrounded by a ventral fringe of setae that partly overlap the triturative area (see picture on the left).

***Parschisturella carinata* (Schellenberg, 1926) (opportunistic necrophage)**

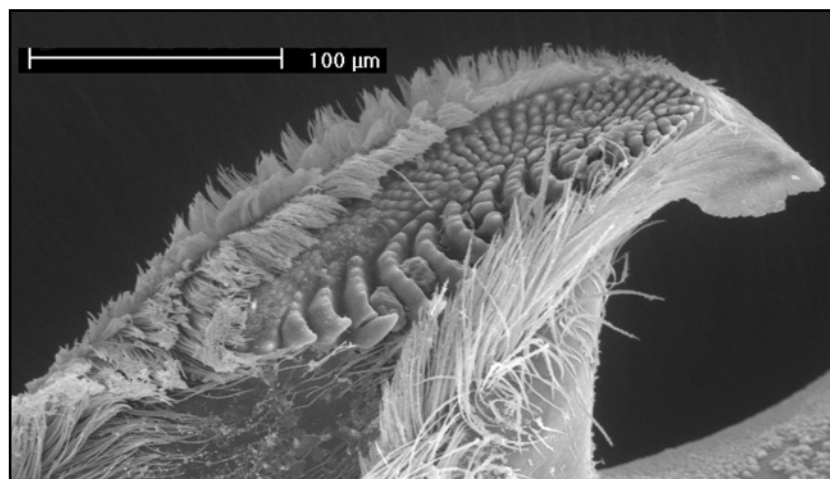
Examination of foregut and gut contents. Gut content observations revealed a diet composed mainly of crustaceans (see picture on the right). Nevertheless, this species is commonly observed in baited traps and in this case has the gut full of bait. This suggests a necrophage tendency, at least in an opportunistic way.



Mandible morphology. Incisor process is smooth and its edge is rather sharp and flanked by a single cusp at each end. The slightly concave *corpus mandibulae* is bordered by a row of (7-8) thick spines. The left mandible bears a weak digitiform apically bidentated *lacinia mobilis* (see picture on the right).



Tall molars are highly provided with setae and the oval tritritative area displays impressive series of deep toothed ridges and rasp-like structures (see picture below).



4.4. Discussion

The feeding type of any organism can be assessed in different ways, according to the chosen approach. Regarding the gut composition, distinction can be made among herbivory, detritivory and carnivory. Regarding the size of the ingested food, it is possible to distinguish between microphagy and macrophagy. The third way to assess the trophic category depends on the feeding behaviour of the organisms and, it is possible, for example, to discriminate between predation and necrophagy among carnivores.

Herbivorous species

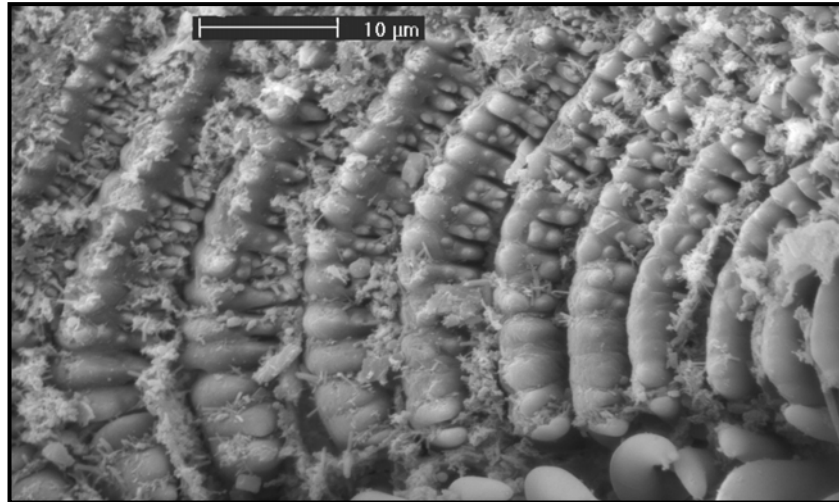
Among the species considered in this work, four of them can be classified in the herbivores: *A. richardsoni*, *O. n.sp.*, *O. walkeri* and *D. furcipes*.

The first species is a microphage feeding mainly on phytoplankton items whereas the three other species consuming essentially macroalgae tissues are categorized as macrophages. These macroherbivores show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The left mandible of the three species is also provided with a strong denticulate *lacinia mobilis* which probably works as an additional cutting edge.

Recently, the origin, function and phylogenetics implication of *lacinia mobilis* have been reconsidered. In 1982, Dahl & Hessler reaffirmed Boas' (1883) hypothesis of a spine-row origin for Peracarida *lacinia mobilis*. In 2002, Richter et al. approved it for the right mandible but for the left mandible, a separation from the incisor process could be more probable - although an origin from the spine row could not be totally excluded. In typical peracaridan biting, the right incisor process enters the gap between the left incisor and the left lacinia, which glides into the gap left between the right incisor and the right lacinia, where the latter is present. The function of

the lacinia in biting appears to be three- or possibly fourfold. It contributes to cutting, it helps guide the incisor processes into the right planes and to lock them into their final closing position. Probably a toothed or spiny lacinia also helps to hold food particles in place during the bite (Dahl & Hessler 1982, Watling 1993).

In macroherbivores, the molar area is provided with strongly denticulate ridges, necessary to triturate the tough macroalgal tissue. The picture below shows *Oradarea* n. sp. molar details.



The diatom consumer, *A. richardsoni*, has a less incurved and elongated incisor process which is also stouter. The molar ridges are few and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae.

Following their diet composition, the new species of the genus *Oradarea* seems to feed preferentially on brown macroalgae. Indeed, a clearly different diet composition has been observed following the offered baits in the traps. When the bait consisted of pieces of algae of the genus *Desmarestia*, the gut was completely filled with plant fragments. Meanwhile, when pieces of the

red algae (*Iridea* sp.) were offered, the gut content was only composed of mineral particles and diatoms. This preferential consumption of *Desmarestia* is not surprising as Amsler et al. (1998) have demonstrated the development of chemical defenses against herbivory for the species *Iridea cordata*. Furthermore, as the repartition area of Desmarestiales (down to 90-100 meters depth, the limit of the phytal zone) is deeper than the one of the genus *Iridea* (from 0 to 10 meters depth), the probability to find those brown algae at 400 meters depth (the sampling depth) is higher. So, the presence of herbivore species in rather deep zones (400 meters depth) is not surprising as the contribution of drifted macroalgae to the organic matter in the deep basins of Admiralty bay is rather high (Fischer & Wiencke, 1992).

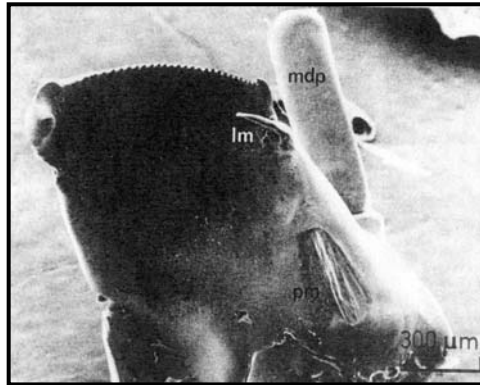
Specialist carnivore species

According to their gut contents, *Epimeria similis* and *Iphimediella cyclogena* are both specialist consumers. The first is considered as a cnidarian-feeder (gut contents essentially composed of cnidocysts and hydroid perisarc fragments), and the second consumes mainly holothurians (high amount of ossicles in gut). However, if each species mandibles are compared with those of other Antarctic species which also feed exclusively on cnidarians or holothurians, as respectively, the iphimeriid *Maxilliphimedia longipes* and the stilipediid *Bathypanoploea schellenbergi* (Coleman 1989a, 1990b), totally different morphologies are observed. These different morphologies are summarized in the following Table as well as *M. longipes* and *B. schellenbergi* mandibles are illustrated in pictures provided by Coleman (1989a, 1990b).

From these observations, one could conclude that to classify an animal as a cnidarian feeder is not restrictive enough, this phylum being composed by organisms with very different structures. In this case, *E. similis* and *M. longipes* must be classified respectively as consumers of hydrozoans and anthozoans respectively. In the latter, gut contents are characterised by the

presence of nematocysts: spirocysts - typical of Hexacorallia, and mastigophores which can frequently be found in Anthozoa and Hydrozoa (Coleman 1989a) whereas *E. similis* gut is essentially composed of perisarc fragments and nematocysts of hydrozoans. The discrepancies in mandible morphology could be explained by the consumption of these different organisms.

In *M. longipes* (see picture on the right from Coleman, 1989a), the remarkable absence of hair-like setae and the smooth aspect of the setae present could be an adaptation to the food source. Setose mouthparts and feather-like setae would



easily be embedded together by the mucus of anthozoans. Furthermore the long cutting edge of their incisor processes can cut larger pieces of prey and the rudimentary molars are not able to triturate food. This could point to very soft food (Coleman 1989a). On the other hand, *E. similis* well-toothed incisors and tall and strongly ridged molars are more adapted to harder kind of food as hydrozoans perisarc.

The dissimilarities in mandible morphology of both holothurian feeders considered in this work: *B. schellenbergi* and *I. cyclogena* is also surprising. Holothurians are a quite uncommon food source for invertebrates. Their integument is leathery with embedded ossicles. On the other hand, their reduced motility makes them a rather ideal prey for other slow predators. Some seastars and among the gastropods, some genera of the prosobranch

family Eulimidae have been observed feeding on holothurians (see references in Coleman 1990b).

B. schellenbergi appeared to be the first “food specialist” feeding on holothurians in the Antarctic. Its mouthparts are interpreted to be highly adapted to cope with the tough tissues of these echinoderms (Coleman 1990b). Its mandibles are remarkably stout. The incisors are strongly serrate, both bearing a *lacinia mobilis*; the left one, also well-toothed, might act as a third cutting edge. This highly integrated cutting mechanism would enable *Bathypanoptea* to cut such firm tissue as the body wall of holothurians. In this species, the molar is reduced so that the reduction of the food in little



pieces relies solely on the actions of the incisors and their laciniae. The picture on the left displays the left incisor process and its *lacinia mobilis*.

Although they seem to rely mainly on the same food source, *Iphimediella* mandible morphology is completely different. As summarized in Table 3.2., the mandibular body is elongated and the incisors are much narrower. Both incisor processes are toothed (10 cusps) and bear a *lacinia mobilis*. But, with such a smooth structure, none of the *lacinia mobilis* could help in cutting tissue as tough as holothurian body wall is. Furthermore, in view of the reduced molar process, the food reduction can not rely only on them. The question is: how do they feed on holothurians? One hypothesis could be that they actually scavenge on rotting holothurians and that the process of decomposition make the tissues softer and easier to cut.

Table 4.2. Summary of the mandible morphological differences between specialist consumers

	CNIDARIAN CONSUMERS		HOLOTHURIAN CONSUMERS	
	<i>E. similis</i>	<i>M. longipes</i>	<i>I. cyclogena</i>	<i>B. schellenbergi</i>
Mandible	- stout	- stout	- elongated	- stout
Incisor & lacinia mobilis (l.m)	- normal - strong teeth - strong and toothed left <i>l. m</i> - weak right <i>l. m</i> - seta row	- broadened - weak teeth - both <i>l.m.</i> are vestigial - no seta row	- very narrow - longitudinally toothed - strong and smooth left <i>l.m</i> - weak right <i>l. m.</i> - no seta row	- normal - strongly serrate - strong and toothed left <i>l. m</i> - weak right <i>l. m.</i> - seta row
Molar	- strong - smooth ridges - fringe of setae	- vestigial	- small fleshy lobe without any ridges and setae	- reduced

Opportunistic predator

According to its gut contents and feeding behaviour observations, *Eusirus perdentatus* is a true predator which seems to be able to switch its diet following the food availability (crustaceans, polychaetes). The most characteristic feature of *E. perdentatus* mandibles is their tall molar bearing a high and small triturative area provided with rasplike structures. The reduced crushing area could explain the rather large food items observed in the gut contents. This ability to ingest big parts of prey could facilitate a fast predation.

Opportunistic necrophages

Besides all other food sources, there is strong evidence that large food falls play a significant role in the vertical flux to the sea bottom, too. On the one hand, there are reports of the encounter of such large food items on the sea floor such as big marine mammal carcasses, fishes, large pelagic invertebrates or their remains (Smith *et al.* 1989, Jones *et al.* 1998, Klages *et al.* 2001). On the other hand, well developed associations of highly mobile scavengers (mainly lysianassoid amphipods) are present on shelf and deep sea bottoms throughout the world oceans. In this context lysianassoids have evolved morphological, physiological and behavioral traits which seem to enable them to rely on this food source. According to Dahl (1979), three adaptations are necessary for efficient carrion feeding. The first adaptation is the development of efficient chemoreceptors to detect and locate carrion. Secondly the ability to feed on large, muscular food items, such as squid, fish or marine mammals by the use of adapted mandibles characterised, briefly, by a wide and sharp incisor edge, a bowl-shape *corpus mandibulae* and a non-tritulative molar (Dahl 1979, Sainte-Marie 1984). Lastly, necrophage lysianassoids seem to solve the starvation problem due to the rarity of their food sources by storing large quantities of carrion in capacious guts.

The scavenging lysianassoids have evolved along two divergent lines represented by the genera *Hirondellea-Eurythenes-Paralicella* and *Orchomene* (Dahl 1979). The former group appears to be the strict (obligate?) necrophage group, the latter being more opportunistic in their feeding. Regarding their mandible morphology, although the basic plan is similar, their mandible features are quite different, and their gut contents analysis, the lysianassoid species considered in this work, *T. murrayi* and *P. carinata*, would belong more probably to the second group. Although it has been classified as a true necrophage by Dauby et al. (2001), our new gut content analyses of *P. carinata* (several individuals were full of crustaceans' remains) and furthermore the extreme development of its molar (tall and strongly ridged) obviously enabling this species to feed on other items than carrion, suggest a more opportunistic feeding behaviour. Besides its necrophagous behaviour, *T. murrayi* is also a predator and has already been observed killing and eating others crustaceans and even fishes (Dauby et al. 2001).

So, for both species the molar development suggests that these animals rely on a broader dietary regime. In any case, the smooth and sharp incisor of lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

Acknowledgements

We would like to thank Prof. W. Arntz (AWI, Bremerhaven) for his invitation to participate to the EASIZ cruises, to Officers and Crews of the R.V. *Polarstern*, and Colleagues of the AWI (Bremerhaven, Germany), who helped in collecting and sorting samples. Dr Y. Scailteur (IRScNB) is acknowledged for his work in gut content analyses. Particular thanks to Julien Cillis (IRSNB, Brussels) and Mathieu Poulicek (ULg, Liège) for their great help in the scanning electronic microscopy work. The first author received a grant from the Belgian "Fonds de la Recherche pour l'Industrie et l'Agriculture" (FRIA). The present research was performed under the auspices of the Scientific Research Programme on Antarctic (Phase IV) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC contract n° A4/36/BO2).

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CHAPTER 5: THE CRUSTACEAN SCAVENGER GUILD IN ANTARCTIC SHELF, BATHYAL AND ABYSSAL COMMUNITIES

After De Broyer C, Nyssen F, Dauby P (2004) Deep-Sea Research,
Part II: 51: 1733-1752

Abstract

Peracarid crustaceans form a significant part of the macrobenthic community which is responsible for scavenging on large food falls onto the sea floor. Although several studies are available about scavengers from tropical and temperate seas, very little information has been published about such species living in Antarctic waters, particularly at greater depths. The present paper is based on a collection of 31 baited trap sets deployed in the Weddell Sea, Scotia Sea and off the South Shetland Islands, and presents results on the geographical and bathymetric distribution of the different taxa and on the ecofunctional role of scavengers.

Some 68,000 peracarid crustaceans from 62 species were collected. About 98% of individuals belonged to the amphipod superfamily Lysianassoidea, and 2% to the isopod family Cirolanidae. Of these species, 31, including 26 lysianassoids (1,400 individuals), were collected deeper than 1000 m.

High species richness was discerned for the eastern Weddell Sea shelf compared with other Antarctic areas. The Antarctic slope also seems to be richer in species than other areas investigated in the world, while in the abyss, scavenger species richness appears to be lower in Antarctica. A richness gradient was thus observed from the shelf to the deep. For amphipods, a number of species extend their distribution from the shelf to the slope and only one to the abyssal zone.

Amphipod species showed degrees of adaptation to necrophagy. The functional adaptations of the mandible and the storage function of the gut are discussed. Feeding experiments conducted on lysianassoid species collected at great depths and maintained in aquaria showed a mean feeding rate of about 1.4 to 4.1 % dry body weight.day⁻¹, which is consistent with data obtained from other species.

5.1. Introduction

The scavenger guild plays a key role in deep-sea benthic communities by rapid recycling and dispersing organic falls of all sizes, from small plankters to whales (e.g. Gage and Tyler 1991, Britton and Morton 1994).

In the Antarctic seas, the existence of an abundant and active scavenger fauna was noticed by early Antarctic marine investigators. Observing the large catch of lysianassid amphipods attracted quickly to baited nets at Cape Adare during the National Antarctic Expedition 1901-1904, Hodgson (in Walker 1907) wrote: "*The trap contained about 10,000 of these amphipods.... Four fish were in the trap, one of them had been reduced to an absolute skeleton; on another the amphipods hung by their 'teeth' in a compact mass, completely concealing their victim. Its skin had disappeared, and I judged also a millimetre of flesh.... the other two fish were presumably waiting their turn.*"

These early collections were mostly opportunistic. With the establishment of permanent coastal Antarctic stations, baited traps have been used more systematically to collect necrophagous invertebrates (e.g. Hurley 1965, Arnaud 1970, Bruchhausen et al. 1979, Rakusa-Suszczewski 1982, Nagata 1986, Presler 1986, Slattery and Oliver 1986, Moore 1994). These catches have provided data on the composition, ecology and biology of scavengers, as well as the discovery of species new to science (e.g. Hurley 1965, De Broyer 1985a, Nagata 1986). Most of this sampling was done at depths shallower than 150 m. Attempts to collect scavengers on the deep Antarctic continental shelf, which extends to an average depth of 450 m and, in places, to over 1000 m depth (Clarke and Johnston, 2003), have been relatively few (Arnaud 1970, De Broyer and Klages 1990, De Broyer et al. 1997, 1999, Takeuchi et al. 2001).

Baited trap sampling led to the discovery of an unexpected vagile benthic fauna of fish and crustaceans under the Ross Ice Shelf at a distance of 400

km from the sea, under ice 415 m thick (Bruchhausen et al. 1979, Lipps et al. 1979, Stockton 1982).

In the deep sea, bathyal and abyssal trap sampling was initiated by the Prince of Monaco as early as 1888 and provided new, and sometimes giant, species of crustaceans and fishes (Richard 1934, Chevreux 1935, De Broyer and Thurston 1987). Much later, baited cameras revealed the existence of a very active guild of mobile necrophages in the deep sea which attracted much interest (e.g. Isaacs and Schwartzlose 1975, Hessler et al. 1978, Gage and Tyler 1991, Britton and Morton 1994). In the Antarctic deep sea, attempts at baited trap collecting have, so far, been extremely few: two operations were reported by Bowman and Manning (1972) from north of Amundsen Sea at depths of 4930 and 5045 m and one single operation at 3186 m off Queen Maud Land was undertaken by Takeuchi et al. (2001).

During the *Polarstern* EASIZ campaigns (1996 & 1998) in the Weddell Sea baited traps were used systematically to complement the catches made by other gears in order to obtain a more complete representation of the shelf and slope assemblages at the so-called “integrated stations” (Arntz and Gutt 1997, 1999, De Broyer et al. 1997, 1999). These trap operations collected mobile scavengers (sometimes in large number) that were not, or only rarely, sampled by other gears such as trawls, dredges, epibenthic sledges, box-corers and deep plankton nets.

In addition, investigations of the Antarctic deep sea have recently been conducted during the *Polarstern* ANDEEP cruises in 2002 in the Scotia Sea, the western Weddell Sea and the South Sandwich Trench (Brandt et al. 2003, De Broyer et al. 2003). These bathyal and abyssal investigations involved a series of successful deep-sea trapping operations.

The results of these *Polarstern* campaigns in terms of composition and bathymetric distribution of the crustacean scavenger guild are reported herein and Antarctic shelf and deep sea faunules are compared. In addition, to investigate the role of the scavenger guild in Antarctic shelf communities and

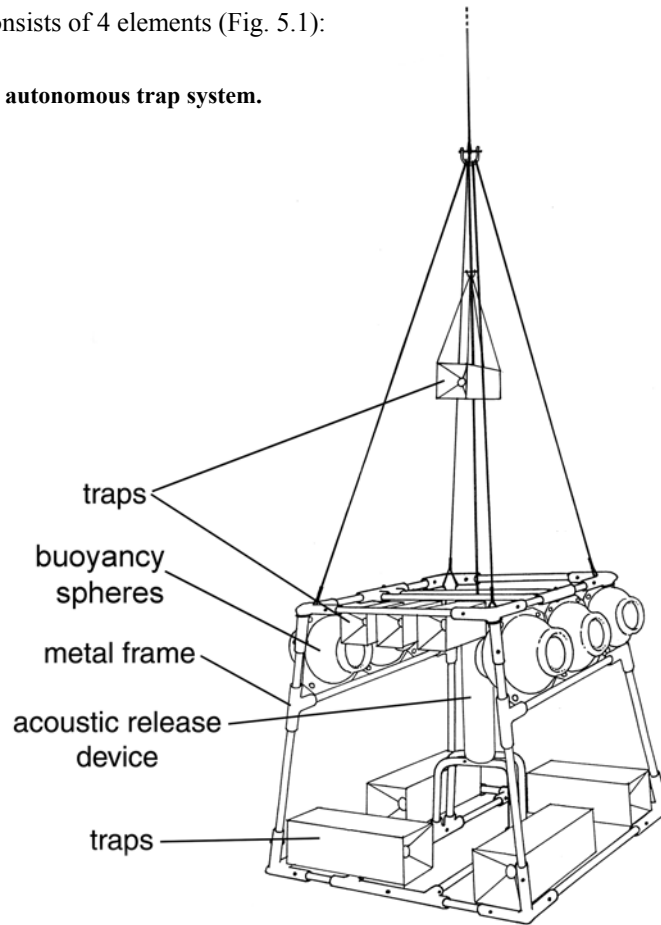
to complement data previously obtained from gut content analyses (Dauby et al. 2001a, b), results of feeding experiments on necrophagous amphipods are presented.

5.2. Material and Methods

5.2.1. THE AUTONOMOUS TRAP SYSTEM

All scavengers were sampled using an 'autonomous trap system' (ATS), based on the system developed at IFREMER, Brest (GuenneGAN and Martin 1985). It consists of 4 elements (Fig. 5.1):

Fig. 5.1. The autonomous trap system.



1. A brass trapezoidal frame (about 1 m³) on which are fixed various baited traps, either in direct contact with bottom or held one metre above. "Box traps" are metal rectangular frames of different sizes (7 or 22 l), covered with nylon gauze of 500 µm, with two inverse conical openings (diameter: 2 or 4 cm). Their upper side can be opened for rapid retrieval of collected animals.
2. A buoyancy package made of sets of high pressure 10" or 17" glass balls (50 and 260 N buoyancy, respectively) attached directly to the frame and a few metres above it.
3. A deep-sea acoustic release (Ix-Sea Oceano Instruments, Brest, France).
4. Disposable ballast made of iron plate and anchor chains.

Traps were baited (preferably) with notothenioid fish when available, or with other fish or beef meat (from about 200 to 600 g, depending on trap size). Bait was usually wrapped in nets (5 mm mesh) in order to prevent too rapid consumption and so increase the time over which it remained attractive. The system was deployed and retrieved after 1 to 5 days (preferably 48 h) on the bottom (Table 5.1). A low-frequency acoustic signal sent from the ship activated release of the ballast and the ATS was returned to the surface by the buoyancy.

The ATS has provided healthy individuals of necrophagous species that could be reared in aquaria and kept alive for as long as two years.

5.2.2. SAMPLING SITES

The material was collected with the ATS during several cruises of the German icebreaker *Polarstern* in the Southern Ocean:

2 operations (using classical line mooring traps) during the EPOS leg 3 cruise, January-February 1989, in the eastern Weddell Sea (De Broyer and Klages, 1990);

6 operations during the EASIZ I cruise, January-March 1996, in the eastern Weddell Sea (De Broyer et al. 1997);

15 operations during the EASIZ II cruise, January-March 1998, in the eastern Weddell Sea and off South Shetland Islands (De Broyer et al. 1999). In addition to ATS catches, two samples were collected from a classical fish trap, at stations 152 and 266.

6 operations during the cruises ANDEEP 1 and ANDEEP 2, January-March 2002, in the southern Drake Passage, the western Weddell Sea and the Scotia Sea (De Broyer et al. 2003).

Sampling data are presented in Table 5.1. and sampling locations are shown in Fig. 5. 2.

Fig.5.2. Location of the 29 trap deployments. Circles and triangles indicate stations lower and deeper than 1000 m, respectively.

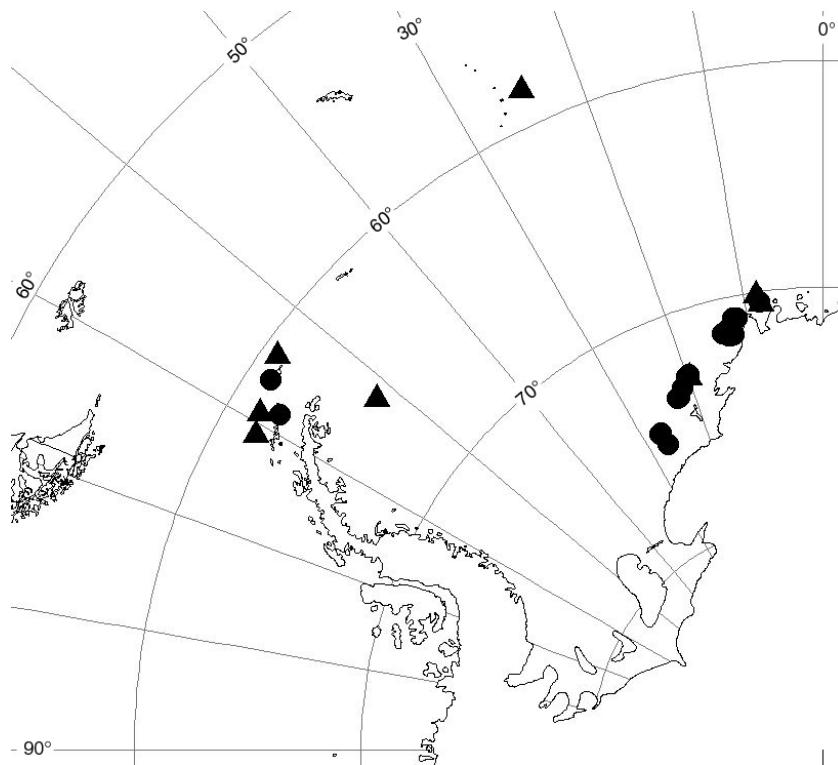


Table 5.1.
Station data for 29 autonomous trap system operations and two fish traps. Italic rows correspond to stations deeper than 1000 m.

Cruise	Station	Date	Area	Location		Depth (m)	Soak Time (h)	Number of specimens
				°S	°W			
EPOS	228 (T2)	28.01.89	Halley Bay	75°14.4'	26°42.1'	399	70	3500
	275 (T4)	15.02.89	Kapp Norvegia	71°39.5'	12°04.4'	236	50	
EASIZ I	04 (T4)	20.02.96	Kapp Norvegia	71°40.6'	12°31.0'	421	132	2924
	05 (T1)	06.02.96	Kapp Norvegia	71°40.2'	12°45.3'	223	23	576
	06 (T2)	07.02.96	Kapp Norvegia	71°31.5'	13°31.4'	234	74	2619
	12 (T3)	13.02.96	Vestkapp	73°15.7'	21°04.8'	791	65	769
	28 (T5)	26.02.96	Kapp Norvegia	71°29.6'	12°21.2'	219	74	2848
	30 (T6)	01.03.96	<i>Atka Bay</i>	<i>70°01.0'</i>	<i>08°16.5'</i>	<i>2009</i>	<i>86</i>	<i>818</i>
EASIZ II	11/25 (T1)	26.01.98	Drescher Inlet	72°50.8'	19°55.5'	377	38	25365
	27/76 (T2)	28.01.98	Kapp Norvegia	71°19.0'	12°24.2'	171	103	10528
	38/75 (T3)	29.01.98	Kapp Norvegia	70°59.0	11°09.1	389	82	765
	094/119 (T4)	05.02.98	Vestkapp	73°35.7'	22°23.4'	813	50	788
	102/122 (T5)	05.02.98	Vestkapp	73°36.0'	22°00.5'	396	46	516
	138/155 (T6)	09.02.98	Halley Bay	74°39.8'	27°13.1'	798	39	3434
	152 (FT)	11.02.98	Halley Bay	74°36.8'	26°53.9'	597		
	160/179 (T7)	11.02.98	Halley Bay	74°40.0'	26°57.9'	403	38	4188
	202/233 (T8)	18.02.98	Kapp Norvegia	70°57.0'	11°40.6'	808	58	401

Cruise	Station	Date	Area	Location		Depth (m)	Soak Time (h)	Number of specimens
				°S	°W			
	203/234 (T9)	18.02.98	Kapp Norvegia	70°58.8'	11°39.4'	442	58	787
	251/267 T10)	22.02.98	Drescher Inlet	72°47.8'	19°31.4'	895	66	1820
	255/268 (T11)	23.02.98	<i>Drescher Inlet</i>	72°48.4'	19°39.6'	1453	58	1642
	266 (FT)	25.02.98	Drescher Inlet	72°50.5'	19°21.8'	419		
	279/283 (T12)	28.02.98	<i>Atka Bay</i>	70°24.1'	07°52.2'	1136	48	75
	280/284 (T13)	28.02.98	<i>Atka Bay</i>	70°27.4'	07°55.9'	550	48	2085
	291/312 (T14)	14.03.98	King George Isl.	62°16.6'	58°15.8'	798	57	451
	292/315 (T15)	14.03.98	King George Isl.	62°11.3'	58°20.2'	414	58	
ANDEEP 1	46	29.01.02	<i>Elephant Isl.</i>	60°39'	53°59'	2926	14	44
	83	07.02.02	Elephant Isl.	61°07'	56°09'	349	72	8597
	100	13.02.02	<i>King George Isl.</i>	61°25'	58°54'	2280	57	171
	114	17.02.02	<i>King George Isl.</i>	61°46'	60°45'	2754	54	36
ANDEEP 2	131	05.03.02	<i>N-W Weddell Sea</i>	65°19'	51°35'	3070	71	129
	139	19.03.02	<i>South Sandwich Trench</i>	58°18'	24°29'	3739	71	1000

5.2.3. FEEDING EXPERIMENTS

Directly after collection, animals were transferred to a cool laboratory (maintained at $-1 \pm 1^\circ\text{C}$), sorted by species and counted. They were then distributed, by groups of 40 to 150, among different aquaria (15 to 200 l) continuously provided with clean fresh sea water.

Several experiments were performed in order to evaluate the feeding rate of four common scavenging Antarctic amphipod species (all lysianassoids, see Table 6). Animals were starved for periods of 9 to 15 days to maximize foregut clearance (as checked from dissected individuals). During this fast, faeces and exuvia were removed daily. After starvation, weighted (and calibrated for dry vs wet weight) food items (pieces of squid or fish) were given *ad lib* every day during experiments lasting 7 to 29 days. Uneaten food was removed after 24 hours, oven-dried and weighed, enabling calculation of mean daily ingestion rates. At the end of last day of experiment, amphipods were sacrificed and oven-dried to obtain their mean individual weight. Results are expressed as $\text{g}_{\text{food-DW}} \cdot \text{g}_{\text{animal-DW}}^{-1} \cdot \text{day}^{-1} \times 100$ (or $\% \cdot \text{day}^{-1}$).

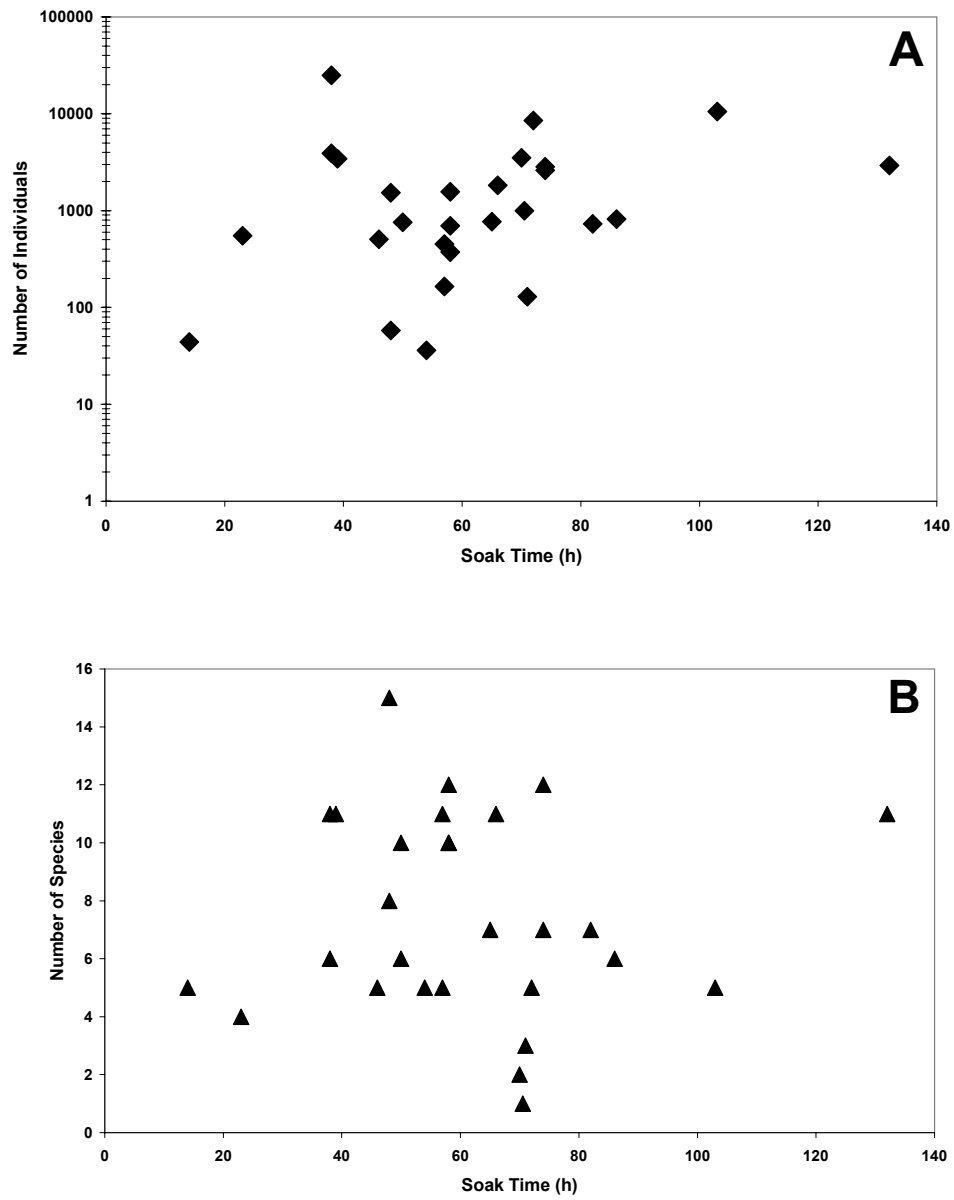
Egestion rates were estimated, in parallel to some feeding experiments, with *Waldeckia obesa* (Chevreux 1905). After a single 24 hour feeding period, a group of animals was placed in nylon gauze baskets (mesh size 2 mm) which allowed faecal pellets to pass through, so to avoid coprophagy. Animals were kept unfed for 5 to 9 days, and faeces were collected twice daily, dried and weighed as above.

5.3. Results and discussion

5.3.1. SAMPLING METHODOLOGY

The ATS is a sampling device which collects roughly "what is scavenging around", *i.e.* the necrophagous organisms able to detect and track the bait odour and living at a distance corresponding to the food odour plume in the water, itself influenced by the direction and velocity of the local bottom current (Sainte-Marie and Hargrave 1987). Several factors, such as bottom topography and related benthic biological community structure, are likely to affect the number and composition of the fauna attracted to bait. Sample size and composition not only depend on these environmental factors, but also on structural ones related to the trap design (mouth opening, mesh size) and relative position of the trap on or above the sea floor. Finally, bait quality and type may attract preferentially some species. The duration of trap deployment has been reported to influence the number of individuals caught, at least initially, when a positive correlation is found (Stockton 1982). However, in our study there was no relationship between the number of individuals or species and soak time for ATS deployments ranging from about 10 to 135 hours (Fig. 5.3.). Possible causes include escape from traps, bait exhaustion, interspecific predation or cannibalism inside the traps (behaviours we observed in restricted aquarium conditions), tidal effects, or simply the local density of the scavenging fauna. Thus the ATS can be considered at best only a semi-qualitative sampler.

Fig. 5.3. Numbers of collected individuals (A) and species (B) vs soak time of the autonomous trap system.



5.3.2. COMPOSITION OF THE SCAVENGER GUILD

The 31 trap sets reported here captured a total of about 70,000 invertebrates from 76 species and 10 specimens of fish from 4 species (Table 5.2).

Table 5.2. Comparison between the number of species and individuals of the different taxonomic groups collected by the autonomous trap system and fish traps at shelf and deep-sea depths.

	ANTARCTIC SHELF	ANTARCTIC DEEP SEA	
	(< 1000m)	(>1000m)	
		EASIZ	ANDEEP
		Eastern Weddell Sea	South Shetland Islands
Campaign	EPOS / EASIZ I & II	South Shetland	Scotia Sea
Locality	Eastern Weddell Sea	Islands	South Sandwich Trench
Depth range	171- 895 m	1139- 2009 m	2280- 3739 m
N trap operations	20	3	5
	N spp (N ind.)	N spp (N ind.)	
CRUSTACEA			
Amphipoda			
Lysianassoidea	37 (~ 65 000)		26 (1374)
Iphimedioidea	2 (4)		2 (2)
Eusiridae	2 (7)		
Melphidippidae	1 (1)		
Stegocephalidae			2 (3)
Isopoda			
Cirolanidae	3 (1547)		1 (4)
Leptostraca	2 (23)		
Ostracoda	2 (1500)		
Copepoda	2(4)		2 (2)
Mysidacea	1 (13)		
Decapoda	1(1)		
MOLLUSCA			
Gastropoda			1 (1)
ECHINODERMATA			
Asteroidea	1(1)		
Ophiuroidea	3(4)		
PISCES	3 (7)		3 (3)

Twenty one trap sets at shelf depths (less than 1000 m) in the eastern Weddell Sea and around South Shetland Islands captured more than 68,000 specimens of crustaceans belonging to 53 benthic and benthopelagic species, 5 specimens of echinoderms and 7 specimens of 3 fish species.

In the deep sea, 8 trap operations on the slope of the eastern Weddell Sea and at bathyal and abyssal depths in the western Weddell Sea, the Scotia Sea and the South Sandwich Trench provided about 1400 crustaceans of 33 species, 1 specimen of a gastropod and 3 specimens of fish.

While the trap samples can be considered representative of the crustacean scavenger fauna, this is not the case for the fish as the traps were suboptimal in terms of size and entrance diameter for collecting them.

Both at shelf depth and in the deep sea (slope and abyssal plain) the bulk of the catches consisted of amphipod crustaceans, in particular lysianassoids. The second dominant group, the cirolanid isopods, was not represented significantly in the deep-sea samples. A few representatives of other amphipod families (Epimeriidae, Iphimediidae, Eusiridae, Melphidippidae, Stegocephalidae) were collected as well as other crustacean groups, namely Leptostraca, Ostracoda, Copepoda, Mysidacea and Decapoda.

The detailed taxonomic composition of the amphipods collected is presented in Tables 5.3. and 5.4. Complete taxonomic references and zoogeographical characterization of the species can be found in De Broyer and Jazdzewski (1993). Within the very diverse superfamily Lysianassoidea, species have been allocated to the different family groups recognized by a recent cladistic analysis (Lowry pers. comm.). On the shelf, a total of 37 lysianassoid species have been collected belonging to 17 different genera. Lysianassoid amphipods are known to comprise a number of scavenger species (e.g. Thurston 1990, Lowry and Stoddart 1989, 1994). Representatives of *Adeliella* and *Allogaussia* were taken in traps for the first time but may be accidental (one unique specimen in each case). Part of the collected species remains to be precisely identified. One new species has been found in each of

the genera *Allogaussia*, *Paracallisoma*, *Pseudorchomene*, *Stephonyx* and *Tryphosella*.

Table 5.3. Amphipod species collected with the autonomous trap system and fish traps at depths shallower than 1000 metres; occurrence by station and depth ranges.

	EPOS	EASIZ I	EASIZ II	Depth range
LYSIANASSOIDEA				
Lysianassidae and Uristidae				
<i>Abyssorhomene charcoti</i> (Chevreux, 1912)		T2		234
<i>Abyssorhomene nodimanus</i> (Walker, 1903)	T4	T2-4-5	T2-4-13	171-813
<i>Abyssorhomene plebs</i> (Hurley, 1965)	T2		T1-5-7-13-14-15	377-798
<i>Abyssorhomene rossi</i> (Walker, 1903)		T4-5	T1-7-9-13	219-550
<i>Adeliella</i> sp.A			152	597
<i>Allogaussia</i> n.sp.1		²	T4	813
<i>Cheirimedon crenatipalmatus</i> Stebbing, 1888		T3	152	389-597
<i>Hippomedon</i> sp.A		T2-5	T6-7-8-9-10-13, 152	219-895
<i>Orchomenopsis cavimanus</i> (Stebbing, 1888)		T4-5	T1 to 10, 13-14, 152	171-895
var.A				
<i>Orchomenopsis kryptopinguides</i> (Andres, 1983)			T3	389
<i>Orchomenopsis pinguides</i> (Walker, 1903)	T4	T2-5	T2-7	171-403
<i>Parschisturella carinata</i> (Schellenberg, 1926)		T1-2-3-4-5	T3-4-5-6-8-10, 152	219-895
<i>Pseudorchomene coatsi</i> (Chilton, 1912)	T4	T4-5	T1-10, 13-14-15, 266	171-895
<i>Pseudorchomene</i> n.sp.1			T4-6-10	798-895
<i>Stephonyx</i> n.sp.1		T3	T4-6-8-10-13	791-895
<i>Tryphosella cf analogica</i> K.H. Barnard, 1932		T3	T6-10	791-895
<i>Tryphosella bispinosa</i> (Schellenberg, 1931)		T2		234
<i>Tryphosella intermedia</i> (Schellenberg, 1926)			T6-7-8-9-10, 152	403-895
<i>Tryphosella longiseta</i> Ren, 1991			T8	808
<i>Tryphosella macropareia</i> (Schellenberg, 1926)		T4	T4-8	421-813
<i>Tryphosella murrayi</i> (Walker, 1903)	T4	T1-2-4	T1-3-7-9-10-13, 266	223-895
<i>Tryphosella</i> n.sp.1			T6	798
<i>Tryphosella</i> sp.A			T4	813
<i>Tryphosella</i> sp.B			T7	403
<i>Tryphosella</i> sp.C			T7	403

	EPOS	EASIZ I	EASIZ II	Depth range
<i>Tryphosella</i> sp.D			T9	442
<i>Tryphosella</i> sp.E		T2-3		234-791
<i>Tryphosella</i> sp.F		T4		421
<i>Tryphosella</i> sp.G		T4		421
" <i>Tryphosella</i> " <i>cicadopsis</i> Schellenberg, 1926			T7-9-13	403-550
" <i>Tryphosella</i> " n.sp.2			T6-13, 152	550-798
<i>Uristes</i> <i>gigas</i> Dana, 1849			T13, 152	550-597
<i>Uristes</i> <i>stebbingi</i> (Walker, 1903)	T4	T2	T2-4	171-813
<i>Waldeckia</i> <i>obesa</i> (Chevreux, 1905)	T2-4	T1-2-3-4-5	T1, 3 to 10, 13, 152	219-895
Eurytheneid family group				
<i>Eurythenes</i> <i>gryllus</i> (Lichtenstein, 1822)		T3	T13-14	550-798
Hirondelleid family group				
<i>Hirondellea</i> <i>antarctica</i> (Schellenberg, 1926)		T1-2-3	T8-13, 152	223-808
Scopelocheiridae				
<i>Paracallisoma</i> n.sp.1			T14	451
IPHIMEDIOIDEA				
Epimeriidae				
<i>Epimeria</i> <i>similis</i> Chevreux, 1912			T10-13, 152	550-895
lphimediidae				
<i>lphimediella</i> <i>bransfieldi</i> K.H. Barnard, 1932			266	419
EUSIROIDEA				
Eusiridae				
<i>Eusirus</i> cf <i>antarcticus</i> Thomson, 1880		T2-5	T3-9, 152	219-597
<i>Eusirus</i> <i>bouvieri</i> Chevreux, 1911		T4	T7	403-421
Melphidippidae				
<i>Melphidippa</i> <i>antarctica</i> Schellenberg, 1926			152	597

Table 5.4. Amphipod species collected with the autonomous trap system and fish traps at depths greater than 1000 metres; occurrence by station and depth ranges.

	EASIZ I	EASIZ II	ANDEEP	Depth range
LYSIANASSOIDEA				
Lysianassidae and Uristidae				
<i>Abyssorhomene rossi</i> (Walker, 1903)		T11		1453
<i>Abyssorhomene scotianensis</i> (Andres, T6 1983)		T11-12	100,114,131	1136-3070
<i>Abyssorhomene sp.A</i>			114	2754
<i>Hippomedon sp.A</i>	T6			2009
<i>Hippomedon sp.B</i>		T11		1453
<i>Orchomenopsis cavimanus</i> (Stebbing, 1888) var.A		T11-12	100,131	1136-3070
<i>Orchomenopsis n.sp.1</i>			46	2926
<i>Parschisturella carinata</i> (Schellenberg, 1926)		T11-12		1136-1453
<i>Pseudorchomene coatsi</i> (Chilton, 1912)		T11	100	1453-2280
<i>Pseudorchomene n.sp.1</i>		T11		1453
<i>Stephonyx n.sp.1</i>		T11-12		1136-1453
<i>Tryphosella cf analogica</i> K.H. Barnard, 1932		T11-12		1136-1453
<i>Tryphosella sp.C</i>		T12		1136
<i>Tryphosella sp.H</i>			100	2280
<i>Tryphosella sp.I</i>			100	2280
<i>Tryphosella sp.J</i>			100	2280
" <i>Tryphosella</i> " <i>n.sp.2</i>		T11		1453
<i>Tryphosinae gen. sp.A</i>		T11		1453
Alicellid family group				
<i>Alicella n.sp.1</i>			100	2280
<i>Paralicella cf caperesca</i> Shulenberger & Barnard, 1976			46	2926
<i>Paralicella n.sp.1</i>			100,114	2280-2754

	EASIZ I	EASIZ II	ANDEEP	Depth range
Eurytheneid family group				
<i>Eurythenes gryllus</i> (Lichtenstein, 1822)	T6	T11-12	46,100,114, 131,139	1453-3739
Hirondelleid family group				
<i>Hirondellea antarctica</i> (Schellenberg, 1926)		T12		1136
<i>Hirondellea n.sp.1</i>			100	2280
Scopelocheridae				
<i>Paracallisoma n.sp.1</i>			100	2280
<i>Scopelocheirus sp.A</i>			46,100,114	2280-2926
IPHIMEDIOIDEA				
Epimeriidae				
<i>Gen. sp.A</i>			46	2926
Iphimediidae				
<i>Iphimediella sp.A</i>	T6			2009
Stegocephalidae				
<i>Gen.sp.C</i>	T6			2009
<i>Gen.sp.D</i>	T6			2009

In the deep sea, 26 lysianassoid species from 15 genera were found, with one new species in each of the following genera: *Alicella*, *Hirondellea*, *Orchomenopsis*, *Paralicella* and “*Tryphosella*” in addition to the 4 new species occurring also in the shelf zone.

Single species of Epimeriidae and Iphimediidae have been found in each depth zone. There is no previous record of Epimeriidae in baited traps except for *Epimeria cf. cornigera* (Jones et al. 2003) and *Epimeria similis* (Dauby et al. 2001a). Stomach content analysis of the latter species by the same authors revealed the presence of various food items such as cnidocysts of hydrozoans and actiniids, sponge spicules, polychaete setae and planktonic cells (diatoms and foraminifers) but also of pieces of fish flesh in individuals captured in traps. Iphimediidae have never been taken in baited traps and their trophic ecology generally characterises them as being specialist micropredators (Coleman 1989a, 1989b, Dauby et al. 2001a). They were probably caught accidentally in traps.

Few Eusiridae are regular scavengers (e.g. Chevreux 1935, Vader 1972, Bowman 1974). Some *Eusirus* species have been recorded in traps in Admiralty Bay, King George Island (De Broyer unpubl.) and on the shelf off Enderby Land (Takeuchi et al. 2001). Examination of feeding behaviour and stomach contents showed that *E. cf. antarcticus*, for instance, is a selective macropredator able to feed partially on carrion (Dauby et al. 2001a).

Melphidippa antarctica is a passive suspension feeder (Dauby et al. 2001a) and the unique specimen was quite probably collected accidentally in trap.

Stegocephalidae are mostly micropredators associated with diverse benthic sessile invertebrates, while some species have been reported to be occasional scavengers (Berge and Vader 2003). They are, however, not taken commonly in traps except for some species of *Andaniotes* and *Austrocephaloides* (Berge and Vader 2001, Berge *pers. comm.*). Takeuchi et al. (2001) found *Parandania boeckii* (Stebbing 1888) and *Euandania gigantea* (Stebbing 1883) in their abyssal trap off Enderby Land. Both species are meso- or

bathypelagic and rarely if ever taken in baited traps. Some specimens of *Euandania* were also found by Thurston (*pers. comm.*) in bathyal and abyssal trap catches in the Atlantic Ocean.

Species diversity is high in the scavenger guild on the Antarctic shelf (eastern Weddell Sea), in particular in crustaceans, i.e. in comparison with catches at shallower depths, such as those reported by Presler (1986) in the sublittoral of King George Island, who found 5 species of amphipods and 2 of isopods. Nemerteans, gastropods, and echinoderms (asteroids, ophiuroids, echinoids and holothuroids) occur frequently in traps at depths of less than 100 m (*e.g.* Arnaud 1970, Presler 1986, De Broyer *unpubl.*). These groups were not represented in our catches at shelf, slope or abyssal depths except for five specimens of echinoderms and a single gastropod respectively found on the Weddell Sea shelf and slope.

The higher species richness seems also to hold true when eastern Weddell Sea shelf data are compared with other Antarctic catches at similar depths (*e.g.* Arnaud 1970, Stockton 1982, Nagata 1986, Takeuchi et al. 2001). Arnaud (1970), for instance, found only a few tens of amphipods of two species (*Abyssorchomene plebs* and *A. rossi*), one specimen of two species of pycnogonid and of one species of fish at a depth of 320 m off Terre Adélie. Stockton (1982) recorded five species of amphipods (among which four lysianassoids) and one mysid under the Ross Ice Shelf, while Nagata (1986) collected only four species of lysianassoids near Syowa Station (Lützow-Holm Bay, East Antarctica). Takeuchi et al. (2001) found 7 species of amphipods (6 lysianassoids, 1 eusirid), 2 of isopods (Cirolanidae, Gnathiidae), 1 mysid, 3 ostracods, 1 copepod, 1 leptostracan and 2 species of nototheniid fish in two trapsets on the shelf (171 and 353 m) off Enderby Land. The general composition of the scavenger fauna thus appears quite similar between the eastern Weddell Sea and Enderby Land but more amphipods have been recorded in the former, which may at least partly be due to the larger number of trapsets analysed from the Weddell Sea (18 vs 2).

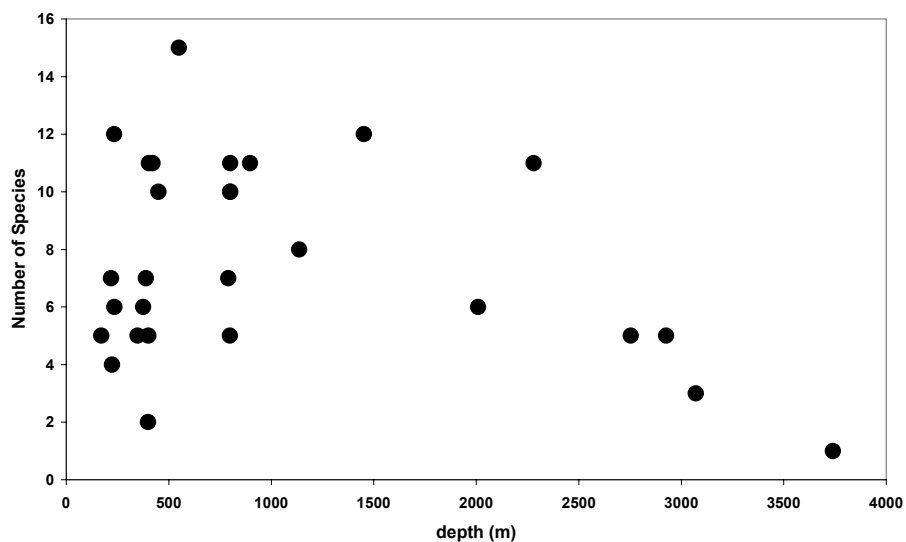
In the Antarctic abyssal waters (3000 m or deeper) the species richness of the scavenger guild appears to be less than documented from abyssal trap collections elsewhere in the world. The three ANDEEP trapsets close to or deeper than 3000 m provided only 5 species of necrophagous amphipods (Table 4) and Takeuchi et al. (2001) reported 5 amphipod and 1 isopod species. In comparison, the 44 trap-sets at 3144-5940 m in the northeastern and tropical Atlantic Ocean analysed by Thurston (1990) yielded 15 different species (13 lysianassids, 1 scopelocheirid, 1 valettiettid), which constitute the largest abyssal trap record. Thurston's record, however, concerned several distinct abyssal plains and a much wider bathymetric range, prospected with many more trap-sets.

On the other hand, the Antarctic slope (1000-3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range. Thirty one amphipod species have been collected (18 in the eastern Weddell Sea) versus e.g. 6 amphipods species (all lysianassoids) on the Gulf of Biscay slope (200-1800 m depth; Desbruyères et al., 1985), 11 amphipod species (9 lysianassoids, 1 eusirid, 1 tironid) found in baited traps by Vinogradov (1997) on the slope of the Norwegian Sea (1690 m) or 5 amphipod species (4 lysianassoids, 1 epimeriid) collected by traps in the deep Cretan Sea (1511-2485 m depth; Jones et al. 2003).

It must be kept in mind in such comparisons that trap sampling is by no means quantitative, as remarked above, and that repeated sampling may yield more species.

The relation between species richness of necrophagous amphipods and depth is shown in Fig. 5.4. This figure clearly shows the variability of amphipod richness in coastal and shelf traps and its reduction from the shelf down-slope to the abyssal zone.

Fig. 5.4. Relation between species richness of necrophagous amphipods and depth.



A number of species occurred on both the shelf and the slope showing in some cases a quite extended level of bathymetry: *Abyssorchomene rossi* (219-1453 m), *Eurythenes gryllus* (550-3789 m), *Hippomedon* sp.A (389-2009 m), *Hirondellea antarctica* (223-1136 m), *Orchomenopsis cavimanus* var.A (171-3070 m), *Paracallisoma* n.sp.1 (451-2280 m), *Parschisturella carinata* (219-1453 m), *Pseudorchomene coatsi* (171-2280 m), *Pseudorchomene* n.sp.1 (798-1453 m), *Stephonyx* n.sp.1 (791-1453 m), *Tryphosella* cf *analogica* (791-1453 m), *Tryphosella* sp.C (403-1136 m), “*Tryphosella*” n.sp.2 (550-1453 m). In the Southern Ocean, *E. gryllus* is the only scavenger species found on the shelf, the slope and in the abyssal zone (see also Takeuchi et al. 2001). The latter species is a panoceanic bathyal (on seamounts, as shallow as 1440 m, Bucklin et al. 1987), abyssal and hadal stenotherm species which can occur far above the sea floor (Thurston 1990). It has been found in both polar regions at bathyal and abyssal depths (e.g.

Bowman and Manning 1972, Paul 1973, Hargrave et al. 1992, De Broyer et al. 1999) and in bird stomachs (see Rauschert 1985).

Arnaud (1970) observed some seasonality in the presence or abundance of several scavengers in the Terre Adélie catches (16 to 120 m): *Waldeckia obesa* was much more abundant in traps in winter than in summer and this could indicate a seasonal shift in diet or a migration. *W. obesa* was abundant in the Weddell Sea at shelf depths (171-895 m) during summer, suggesting migration or local movement as a most like cause (see Bregazzi 1972, Slattery and Oliver 1986).

5.3.3. MORPHOLOGICAL ADAPTATIONS TO NECROPHAGY

Morphological analysis of the amphipod species collected in traps (Tables 5.3. and 5.4.) has shown several types and degrees of adaptation to a necrophagous mode of life, thus confirming previous observations and interpretations (Dahl 1979, Thurston 1979, De Broyer 1983). The typical eco-functional adaptations to necrophagy are summarized briefly in Table 5.5. No attempt is made here to document detailed differences in chemosensory organs (in particular callynophores, see Lowry 1986, Meador 1981) or mechanoreceptors (Klages et al. 2002). The focus is on the morphology of the mandible and the digestive tract.

Table 5.5. Morphological and physiological adaptations of scavenging amphipods with respect to behavioural constraints.

<i>Typical behavioural sequence of scavengers</i>	<i>Morphological and physiological adaptations</i>
Detecting and locating carrion source	Chemosensory organs (callynophores) Mechanoreception organs
Arriving (quickly) to carrion	Good swimming ability
Ingesting (quickly)	Cutting mandible
Storing food	Enlarged foregut or midgut

Typical behavioural sequence of scavengers	Morphological adaptations and physiological
Feeding opportunities	
Unpredictable	Resistance to starvation Reduced metabolism

Mandible morphology appears of primary importance in amphipod evolution in general and in the scavenger feeding types in particular (Dahl 1979, De Broyer 1985b, Barnard and Karaman 1991, Watling 1993). The evolutionary trend toward necrophagy is marked by several transformations of the mandible from the relatively basic type found in the opportunistic scavengers *Orchomenopsis* (e.g. *O. obtusa*; see Olerod, 1975) or *Abyssorchomene* to the types found in the deep sea species that are obligate scavengers *Eurythenes*, *Hirondellea* and *Paralicella* (Dahl 1979, Thurston 1979, De Broyer 1983). The following morphological transformations are considered adaptations to necrophagy:

- widening and sharpening of the incisor cutting edge;
- modification of the molar process from a relatively basic subcolumnar type with oval triturative surface (*Orchomenopsis*; see Olerod 1975, Fig. 62 & 63) to the ridge-shaped type with elongate and reduced triturative surface (*Abyssorchomene*; see Dahl 1979, Fig. 9), and ultimately to the non triturative semitubular or “flap-like” setiferous molar found in *Hirondellea* or *Eurythenes* respectively (see Dahl 1979, Fig. 5 & 6);
- transformation of the flat mandibular body found in *Orchomenopsis* to the strongly bowl-shaped type found in *Eurythenes* or in *Alicella* (see De Broyer and Thurston 1987). Together with the development of the raker spine row and the setal row prolonging the molar, and the widening of the incisor, this adaptation allows relatively large fragments or ships of food to be passed directly into the oesophagus (Thurston 1979, De Broyer and Thurston 1987). In common with the present deep sea material, all the abyssal scavenger species recorded by Thurston (1990) with the exception of *Valettietta gracilis*

have a mandibular molar considerably modified from the basic gammaridean pattern.

Another important adaptation to necrophagy is the development of the storage capacity of either the foregut, *e.g.* in *Abyssorchomene* or the midgut in *Eurythenes*, *Hirondellea* or *Paralicella* (Dahl 1979, De Broyer 1983). The “storing stomodeum” extending along the whole length of the pereion has been found in most lysianassid and uristid species we collected from shelf and deep-sea traps: *Abyssorchomene*, *Hippomedon*, *Parschisturella*, *Pseudorchomene*, *Tryphosella*, *Uristes* and *Waldeckia*. In *Orchomenella* (*Orchomenopsis*) it extends to the fourth pereionite.

Because several steps can be detected along the evolutionary pathway to the necrophagous mode of life in amphipods, it seems obvious from the morphological comparison of the different scavenger groups (in particular: eurytheneids, hirondelleids, alicellids, scopelochiridae) that these adaptations arose independently several times during the evolution within the Lysianassoidea.

Previous studies have shown that baited traps attracted facultative, opportunistic scavengers as well as (presumed) obligate scavengers (*e.g.* Arnaud 1970, Britton & Morton 1994, Dauby et al. 2001a). The distinction between the two categories on the basis of morphological traits is by no means straightforward in amphipods. Mandible and gut morphology can help indicate scavenger status, but only within certain limitations. Eurytheneids, alicellids, some Lysianassidae such as *Waldeckia obesa* are considered to be exclusive scavengers. Within the genus *Hirondellea*, for instance, which has a typical advanced scavenger-type mandible, deep-sea species probably are exclusive scavengers (Hessler et al. 1978). However, the shelf species *H. antarctica* is collected regularly in traps but is supposed to be mainly a micropredator on hydrozoans and sea anemones (Dauby et al. 2001a). *Abyssorchomene plebs* is frequently taken and sometimes is extremely abundant in bottom traps (*e.g.* Rakusa-Suszczewski 1982, De Broyer and

Klages 1990). This species, as well as the less common *A. rossi*, are typical benthopelagic species that are also able to prey on copepods, salps and coelenterates in the water column (Dauby et al. 2001a). These *Abyssorhomene* species can feed on phytoplankton and microzooplankton organisms (Hopkins 1985, 1987) presumably aggregated prior to ingestion (see Riebesell et al. 1991) as these species have no filtering appendages.

Stomach content studies of animals from trap collections, as well as fatty acid and stable isotope analyses (Graeve et al. 2001, Nyssen et al. 2002), have revealed that the opportunistic scavengers may be primarily predators (e.g. *Eusirus antarcticus*, *E. bouvieri*, *Hirondellea antarctica*, *Tryphosella murrayi*) or mainly deposit feeders (e.g. *Uristes gigas*).

5.3.4. BATHYMETRIC DISTRIBUTION

The bathymetric distribution of amphipods collected in traps in the eastern Weddell Sea is given in Fig. 5.5 (next page). The chart is not representative of the complete bathymetric distribution of these species as it does not include depth records from other gears.

In terms of bathymetric distribution, the trap results (Fig. 5.5, next page) may indicate a faunal break for scavenger amphipods at a depth of about 800 to 1000 m in the eastern Weddell Sea that may be related to the shelf break depth. The same faunal limit is suggested by the scavenger isopod distribution (Fig. 5.6).

Fig. 5.6. Bathymetric distribution of cirrolanid isopods collected with the autonomous trap system in the eastern Weddell Sea.

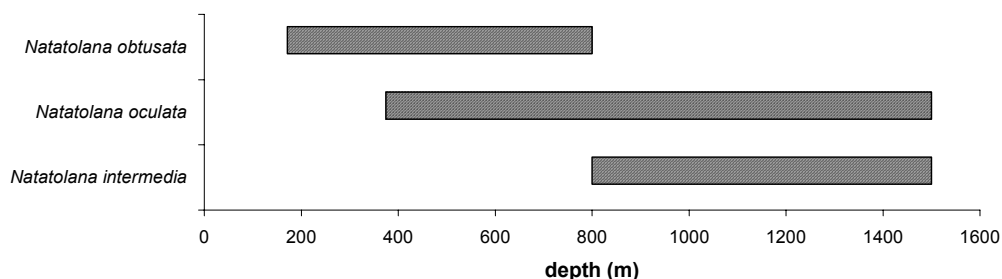
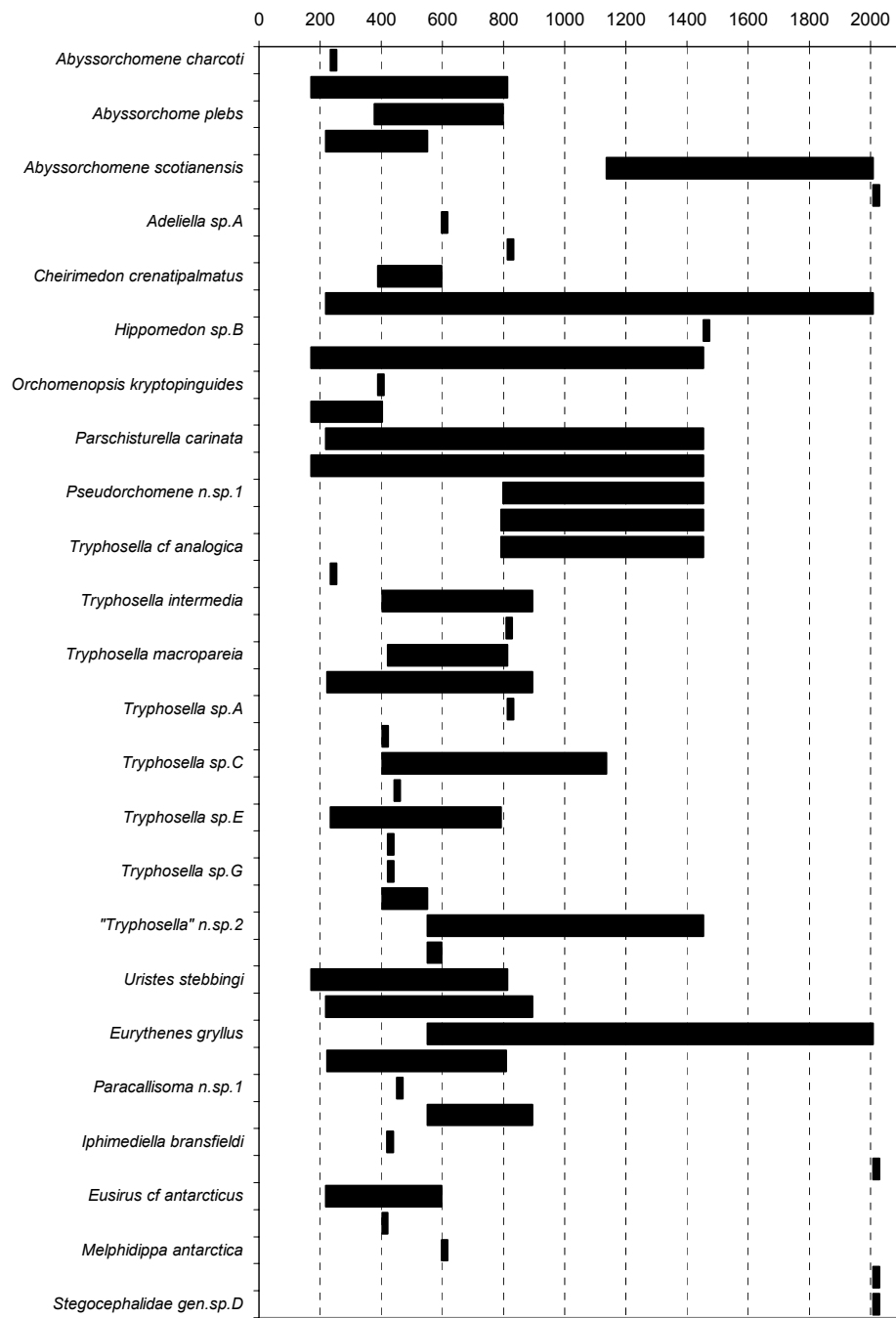


Fig. 5.5. Bathymetric distribution of amphipods collected with the autonomous trap system in the eastern Weddell Sea.



5.3.5. FEEDING EXPERIMENTS

Table 5.6 gives the mean (and range) of the average feeding rates (in % dry weight.day⁻¹) measured during several experiments for the 4 studied species of Lysianassoidea. The egestion rate and digestion efficiency (both in % of ingested food) are given for *Waldeckia obesa*. Available data for other Lysianassoidea are also reported.

Table 5.6. Estimated and reported feeding rates of scavenging lysianassoid amphipods. F: given food, N: number of experiments, FR: feeding rate (%body dry weight.day-1), MS: meal size (% body weight), ER: egestion rate (% food.day-1), DE: digestion efficiency (% food)

species	F	N	FR	MS	ER	DE	reference
<i>Abyssorchomene nodimanus</i>	squid	5	4.1 (2.5 – 5.1)				this study
<i>Parschisturella carinata</i>	squid	5	1.9 (1.3 – 2.7)				" "
<i>Tryphosella murayi</i>	fish	8	2.1 (0.4 – 4.5)				" "
	squid	14	1.4 (0.9 – 4.5)				" "
<i>Waldeckia obesa</i>	fish	3	3.1 (2.6 – 10.4)		33	67	" "
	squid	10	2.2 (1.0 – 7.7)				" "
<i>Eurythenes gryllus</i>	fish			30 – 60			Hargrave, 1985
	fish			up to 150			Meador, 1981
<i>Anonyx sarsi</i>	squid			10 – 37			Sainte-Marie, 1987
<i>Anonyx</i> sp.	squid			10 – 18			Sainte-Marie et al., 1989
<i>Orchomenella pinguis</i>	squid			11 – 33			Sainte-Marie et al., 1989
<i>Onisimus litoralis</i>	squid			9 – 11			Sainte-Marie et al., 1989
<i>Alicella gigantea</i>	fish			12			De Broyer and Thurston, 1987

It appears that feeding rates (averaged for each single experiment) encompass relatively large variations, ranging from 0.4 to 10.4 % \cdot day⁻¹. These variations could be explained partly by the differences in the duration of the experiments (from 7 to 29 days, see Fig. 8), and by the fact that the number of experiments differed from species to species. The mean rate (averaged over all the different experiments), however, was not very different among the four species. The type of food given (squid vs fish) influences this rate but the difference is not statistically significant. However, it has been shown (Moore 1994) that *Orchomenopsis zschau* digested soft tissues far more rapidly than epidermal material.

Fig. 5.7. Day-to-day variations of the mean feeding rate (in % dry weight \cdot day⁻¹) of the scavenging lysianassid *Abyssochomene nodimanus* (group of 50 individuals) during an aquarium experiment. Day 1 is the day following the starvation period.

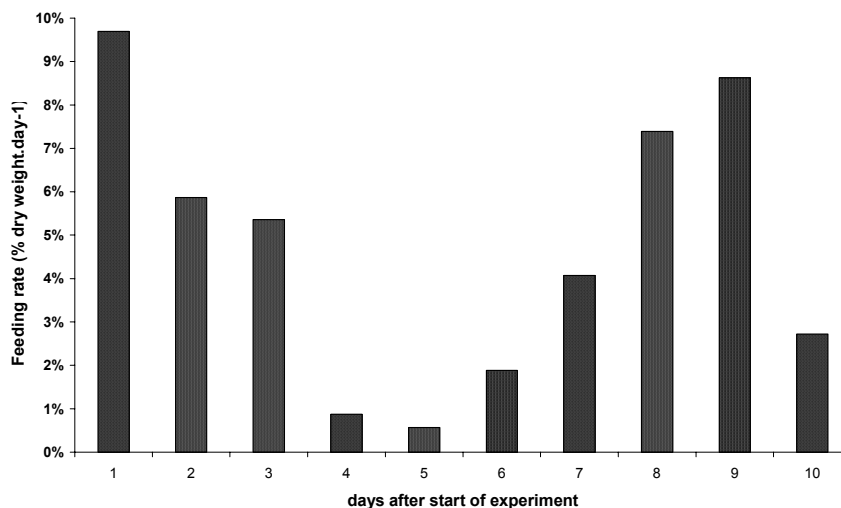
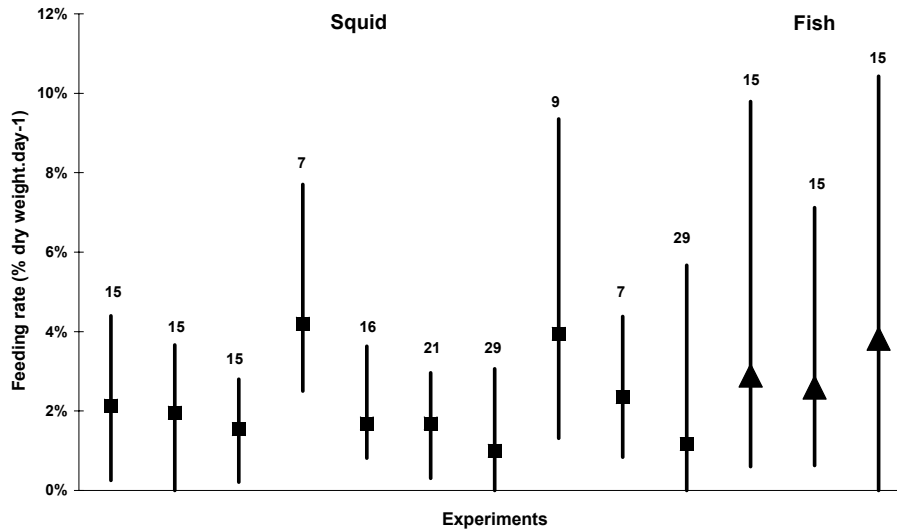


Fig. 5.8. Between experiment variations of the feeding rate (in % dry weight.day⁻¹) of a scavenging lysianassid (*Waldeckia obesa*). Lines show the range of the day-to-day variations; symbols show the mean values (square: fed with squid; triangles: fed with fish). Numbers above the lines give the durations (in days) of experiments.



It is difficult to compare our estimates with literature data, as the latter are expressed in a different way, usually referring to meal size (*vs* body mass) often inferred from *in situ* camera observations (*e.g.* Hargrave 1985). This kind of estimate is made by offering scavengers a large quantity of bait and evaluating the ingested mass over short periods of time. It does not take into account eventual periods of lower feeding activity, such as we observed in aquaria (see below), and is thus a measure of instantaneous ingestion capacity rather than an estimate of feeding rate over longer periods. This may explain the differences between the two sets of values.

The feeding rate of a group of individuals from a given species varied strongly from day to day (Fig. 5.7). Following starvation, lysianassids feed initially at a high rate (up to 15%.day⁻¹ for some species) but afterwards, this

rate decreases gradually over a period of 4 to 8 days, depending on species. A subsequent increase rate is observed, followed again by a decrease. This kind of rhythm, alternating between periods of intense feeding activity and periods of quasi fasting, may be related to the time needed for digesting part of the ingested food or at least for clearance of the foregut. This behaviour could also suggest that tested scavenging amphipods are "topping up" whenever food is available, which would be consistent with a low level of dependency on necrophagy and a plug-flow feeding/digestion strategy (see Penry and Jumars 1987). At the opposite, the gluttonous feeding reported for *e.g.* *Eurythenes* or *Anonyx* in the literature (Table 5.6) is consistent with a high level of dependency on necrophagy and a batch feeding/digestion strategy. It must be pointed out, however, that on the basis of digestive tract observations (Dauby et al. 2001a) species such as *Abyssorchomene nodimanus*, *Parschisturella carinata* or *Waldeckia obesa* have been reported to be obligate –or at least preferential– necrophages.

On the other hand, feeding rates can vary by a factor of 4 to 5 among different experiments on the same species (Fig. 5.8). A huge food intake of bait may occur in the trap (see Table 5.6, meal size), that might be responsible for satiation of some collected animals and for a low feeding rate in aquarium experiments, even after a week-long starvation period. Animals maintained in aquaria can survive unfed for months (Chapelle et al. 1994).

The mean feeding rates, based on our experiments, vary between 1 and 5 % dry weight.day⁻¹, regardless of species. Very few data on digestion and assimilation rates of scavenging lysianassoid amphipods exist in the literature. Sainte-Marie (1992), assuming complete assimilation of the food bolus, calculated that for *E. gryllus* between 8.3 and 17.8 days would be required for complete digestion and assimilation of one meal. Hargrave et al. (1995) estimated from exponential curves fitted to decreases in gut contents of the same species, that digestion would be 95% complete within 15-46 h in the Canada Basin, and within 99-255 h in the Nares and Sohm Abyssal Plain.

Comparing the organic matter in bait and in well-digested gut contents, they estimated a digestion efficiency of 85%, which is not very different from the value we obtained for *W. obesa*, i.e. 67%, using another method. Rapid digestion, associated with liquefaction of food, would enable amphipods to regain mobility as soon as possible after feeding, which is advantageous for these opportunistic feeders in food-poor environments (McKillup and McKillup 1994, Hargrave et al. 1995).

Considering the numerous and diverse benthic fauna recorded on the Antarctic shelf (see Gutt *et al.* 2000) it appears that relatively few species, mostly lysianassoid amphipods, are attracted to baited traps. Similar observations were made in the high Arctic (Legezynska et al. 2000). Some species may occur in huge numbers (*e.g.* Slattery and Oliver 1986, who claimed 264,000 *Abyssorchomene plebs* in a single trap) indicative either of high local densities that are difficult to precisely evaluate, or of low chemosensory thresholds and high mobility allowing some species to congregate from large areas of bottom. The apparently significant role of the scavenger guild in the rapid dispersal of organic matter over the Antarctic shelf and deep-sea bottoms remains to be quantified more precisely.

Acknowledgements

This research was supported by the Scientific Research Programme on the Antarctic (Phases IV and V) of the Belgian Federal Science Policy (contracts n° A4/DD/B02 and EV/36/24A). Samples were collected during the European 'Polarstern' Study (EPOS), sponsored by the European Science Foundation and the Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI, Bremerhaven, Germany), during both EASIZ I & II campaigns (Ecology of the Antarctic Sea-Ice Zone), sponsored by AWI, and during the three consecutive cruises ANDEEP I, ANDEEP II (Antarctic Benthic Deep-

Sea Biodiversity) and LAMPOS (Latin America *Polarstern* Study). We are indebted to the Officers and Crews of RV *Polarstern* for their skillful support of the sampling effort.

We would like to thank Profs. Wolf Arntz and Dieter Fütterer (AWI) and Prof. Angelika Brandt (Univ. Hamburg) for the invitation to participate to these cruises. Thanks are also due to Drs Dieter Gerdes, Michael Klages, Thomas Brey, Julian Gutt (AWI), Brigitte Hilbig (Univ. Hamburg), as well as all colleagues who helped in collecting, sorting and analysing the samples. Our colleagues from IRScNB, Drs. Yves Scailteur and Gauthier Chapelle are acknowledged for their efforts in performing feeding experiments. The ATS system could not be built without the *savoir-faire* of Camille Jamar. Thierry Kuyken and Angelino Meerhaeghe greatly helped in finalising figures and tables. We are grateful to Profs. Geoff Moore (Millport, UK), Mike Thurston (Southampton, UK), Wim Vader (Tromsø, Norway) and an anonymous referee who carefully and critically read and improved the manuscript.

This is ANDEEP contribution No. 20, and MARE publication No. 45.

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CHAPTER 6: AMPHIPODS AS FOOD SOURCES FOR HIGHER TROPHIC LEVELS IN THE SOUTHERN OCEAN: A SYNTHESIS

After Dauby P, Nyssen F, De Broyer C (2003) In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys Publ, Leiden, p 129-134

ABSTRACT

With more than 820 different species, among which about 75% endemics, the amphipod crustaceans form one of the richest animal group of the Southern Ocean. They have colonized most habitats and exhibit very diverse life styles and trophic types. They moreover show a broad size spectrum, with numerous giant species. Despite their importance in terms of biodiversity, very few is known about the role of amphipods in Antarctic trophodynamics. Based on an exhaustive literature survey (more than 300 references), we tried to delineate their importance as potential food for higher trophic levels. About 200 different predators were recorded: 33 invertebrates (from 12 orders), 101 fishes (19 families), 48 birds (11 families) and 10 mammals. Using this vast dataset (total amount of citations close to 1500) and published values about predators' standing stocks and feeding rates, an attempt was made to build up a small model, distinguishing between benthic and pelagic species of both amphipods and predators. The total amount of consumed amphipods was estimated to 60 millions of tons per year for the whole Southern Ocean, *i.e.* the second animal group in importance after euphausiids.

6.1. INTRODUCTION

Recent reviews on the knowledge about marine biodiversity in the Southern Ocean (e.g. Arntz et al. 1997) have stressed for instance the relative importance of some zoological groups, like molluscs and polychaetes, and the predominance of crustaceans. Among the latter, amphipods form obviously the richest group with more than 820 species recorded in the Antarctic and Subantarctic regions (De Broyer & Jazdzewski 1993, 1996). These peracarids have colonised a wide variety of ecological niches, in benthic habitats as well as in the water column (De Broyer et al. 2001), and have developed a large range of feeding strategies, from suspension-feeding to scavenging on big carrion and specialised modes like micro-predatory browsing on invertebrate colonies (Dauby et al. 2001a; Nyssen et al. 2002).

The important faunal diversity of amphipod taxocoenoses is likely to indicate a worthwhile significance of these crustaceans in total benthic or pelagic biomasses, and thus their major role in the trophodynamics of Antarctic ecosystems, as well as consumers than as preys. Total biomass data, and *a fortiori* relative data on amphipods are more than scarce, only available for some restricted areas like the eastern Weddell Sea shelf where amphipods should count for about 5% of the benthic biomass (Gerdes et al. 1992). In the same area, their impact as predators on benthic material has been arbitrarily estimated by Jarre-Teichmann et al. (1997) who supposed they feed for about 80% on detritus. This view was recently revised by Dauby et al. (2001b) who showed, from an extensive study of stomach contents of the most representative species, that their diet was far more complex, planktonic bodies and crustaceans forming the major part of it.

On another hand, the importance of amphipods, either benthic or pelagic, for Southern Ocean higher trophic levels has never been analysed in a global context. If numerous papers have been published on the diet composition of Antarctic top predators (some of which preying on amphipods to a more or

less large extent) very few (Duarte & Moreno 1981, Jazdzewski 1981, Jazdzewski & Konopacka 1999) took the "prey point of view" into account, i.e. the actual role of these crustaceans as food source. The present paper is the first attempt to summarize the available information about Amphipoda as preys. It is based on an exhaustive dataset collected from about 310 published articles wherein amphipods are mentioned to be included in the diet of Antarctic invertebrates, fishes, seabirds or marine mammals.

6.2. RESULTS & DISCUSSION

The bibliographic investigation covers a period running from 1905 till present and concerns the whole Southern Ocean *sensu lato* i.e. including the Sub-Antarctic islands (south of the Sub-Tropical Convergence) but excluding the Magellanic Region. All the collected papers cannot be used in the same way as the included information is not comparable. Old documents were purely qualitative but may be worthy as some amphipod species (such as *e.g. Waldeckia obesa*, Chevreux 1905) were first described from Antarctic fish stomach analyses. Papers since about the fifties were more informative as they contained data about the partition of the different faunal groups in the predator diet, usually as frequency of occurrence (O). More recently appeared more useful articles wherein prey breakdown was expressed in terms of number of items (N), volume (V) or mass (M) fractions. In the last years, finally, papers were published going into more details about prey species identification and their mass repartition in the predator diets. Owing to the editorial policy of the present volume, the set of 310 references will not be listed hereafter.

An amount of about 1500 "records" were registered in the whole dataset. A "record" is defined as the occurrence, in a reference, of a pair [predator species – amphipod species (or family, or sub-order, depending on how precisely preys were determined)]. Several records (up to 60 in *e.g.* Olaso et al. 2000) can thus be found in the same paper.

A total of 176 amphipod species were listed in top predator stomach contents, i.e. more than 20% of the species known for this area. The best represented (super-) families are: lysianassoids, eusirids and epimeriids for gammarideans, and hyperiids and vibiliids for hyperideans (Table 6.1). Curiously, some families well represented in the Antarctic Ocean, like iphimediids, are not commonly found, maybe because of their particular

spinose morphology which should protect them from a heavy predation (Brandt 2000).

Table 6.1: Numbers of species in the different families of Gammaridea, Caprellidea and Hyperidea found in the digestive tract of the Southern Ocean amphipod predators, and corresponding 'records' (see text) in the literature. (+n.d.) indicates non-determined species.

FAMILY	n species	n records
Ampeliscaidae	5 (+n.d.)	11
Amphilochidae	1	1
<i>Ceradocus</i> group	1 (+n.d.)	6
Colomastigidae	1	1
Corophiidae	2 (+n.d.)	6
Dexaminidae	2	10
Eophliantidae	0 (+n.d.)	2
Epimeriidae	8 (+n.d.)	32
Eusiridae	36 (+n.d.)	179
Gammarellidae	4 (+n.d.)	16
Hyalidae	2 (+n.d.)	7
Iphimediidae	2 (+n.d.)	10
Ischyroceridae	4 (+n.d.)	18
Leucothoidae	1 (+n.d.)	5
Liljeborgiidae	2 (+n.d.)	10
Lysianassoidea	29 (+n.d.)	200
Melphidipiidae	1	1
Oedicerotidae	3 (+n.d.)	12
Pardaliscidae	1	1
Phoxocephalidae	3 (+n.d.)	15
Podoceridae	1 (+n.d.)	4
Sebidae	1	1
Stenothoidae	5 (+n.d.)	17
Synopiidae	2 (+n.d.)	8
<i>undetermined</i>		155
Total GAMMARIDEA		728
Phtisicidae	1 (+n.d.)	4
<i>undetermined</i>		10
Total CAPRELLIDEA		14
Brachyscelidae	1	1
Hyperidae	13 (+n.d.)	315
Lanceolidae	1 (+n.d.)	2
Phrosinidae	2 (+n.d.)	28
Phronimidae	1 (+n.d.)	5
Platyscelidae	1	1
Proscinidae	0 (+n.d.)	2
Scinidae	1 (+n.d.)	1
Vibillidae	6 (+n.d.)	102
<i>undetermined</i>		62
Total HYPERIDEA		519

Concurrently, 192 different predators were identified belonging to various zoological groups (Table 6.2). The most numerous records concern fishes

(101 species from 19 families, especially from the notothenioid ones) and seabirds (48 species from 12 families, mainly procellariids and penguins).

Table 6.2: Numbers of species of amphipod predators in the different taxa (from classes to families, depending on groups), and corresponding 'records' (see text) in the literature.

		n species	n records
ANNELIDA	Polychaeta	2	10
MOLLUSCA	Cephalopoda	6	9
CRUSTACEA	Amphipoda	5	8
	Decapoda	2	2
	Isopoda	4	6
	Mysidacea	1	1
ECHINODERMATA	Asteroidea	3	6
	Echinoidea	2	7
	Holothuroidea	4	4
	Ophiuroidea	4	13
CHAETOGNATHA		1	1
TUNICATA	Thaliacea		1
PISCES (101)	Achiropsettidae	1	1
	Artedidraconidae	14	124
	Bathydraconidae	10	43
	Bathylagidae	1	1
	Bovichthyidae	1	1
	Centrolophidae	1	1
	Channichthyidae	7	35
	Congiopodidae	1	6
	Cyclopteridae	4	5
	Gadidae	2	3
	Harpagiferidae	3	38
	Macrouridae	2	2
	Muraenolepidae	2	9
	Myctophidae	11	57
	Notacanthidae	1	1
	Nototheniidae	33	450
	Rajidae	4	7
	Scombridae	1	6
	Zoarcidae	2	8
AVES (48)	Anatidae	2	5
	Chionidae	2	3
	Diomedidae	4	30
	Laridae	5	33
	Muscicapidae	1	1
	Oceanitidae	2	15
	Pelecanoididae	2	30
	Phalacrocoracidae	3	7
	Procellariidae	17	164
	Spheniscidae	8	241
	Stercorariidae	2	9
	<i>undetermined</i>		7
MAMMALIA (10)	Cetacea	5	22
	Pinnipeda	5	17

Amongst invertebrates, the more important amphipod predators are species of polychaetes and echinoderms (starfishes, urchins and brittle stars) in the benthos, and several species of squids in the water column. Very few informative data (Table 6.3) are however available in order to estimate their impact on amphipod populations.

Table 6.3: Examples of predation percentages on amphipods by some selected predators. Amphipod types: Gb: benthic Gammaridea; Gp: pelagic Gammaridea; H: Hyperiidea. Diet estimations: V: per volume; O: per occurrence; N: per number; M: per mass (see text).

Taxa		Predator species	Amphi type	% in diet
ANNELIDA	Polychaeta	<i>Harmothoe spinosa</i>	Gb	99 V
MOLLUSCA	Cephalopoda	<i>Alluroteuthis antarcticus</i>	H	50 O
		<i>Galiteuthis glacialis</i>	H	100 O
ECHINODERMATA	Asteroidea	<i>Labidiaster rupicola</i>	Gb	38 N
	Echinoidea	<i>Sterechinus neumayeri</i>	Gb	4 V
PISCES	Bathyracidae	<i>Gerlachea australis</i>	Gb	13 M
		<i>Cygnodraco mawsoni</i>	Gb	1-12 M
	Artedidraconidae	<i>Artedidracon mirus</i>	Gb	4-72 M
		<i>Artedidracon orianae</i>	Gb	2-80 M
	Harpagiferidae	<i>Pogonophryne marmorata</i>	Gb	3-81 M
		<i>Harpagifer bispinis</i>	Gb	2-96 M
	Nototheniidae	<i>Harpagifer antarcticus</i>	Gb	2-82 M
		<i>Gobionotothen gibberifrons</i>	Gb-H	0-38 M
	Channichthyidae	<i>Notothenia coriiceps</i>	Gb-H	0-88 M
		<i>Lepidonotothen nudifrons</i>	Gb-H	3-38 M
	Myctophidae	<i>Champsocephalus gunnari</i>	H	5-83 M
		<i>Electrona carlsbergi</i>	H	4-27 M
AVES	Diomedidae	<i>Protomyctophum choriodon</i>	H	0-11 M
		<i>Diomedea chrysostoma</i>	H	3-17 O
	Laridae	<i>Sterna vittata</i>	Gb-Gp	3-30 M
		<i>Larus dominicanus</i>	Gp-H	1-38 O
	Oceanitidae	<i>Oceanites oceanicus</i>	Gp-H	1-45 M
		<i>Pelecanoides urinatrix</i>	H	0-17 M
	Procellariidae	<i>Fulmarus glacioides</i>	Gp-H	0-5 M
		<i>Pachiptila desolata</i>	H	0-16 M
	Spheniscidae	<i>Pterodroma spp</i>	Gp-H	0-5 M
		<i>Eudyptes chrysocome</i>	H	0-3 M
		<i>Eudyptes chrysolophus</i>	Gp-H	2-67 M
		<i>Pygoscelis papua</i>	Gb-Gp	0-4 M
MAMMALIA	Cetacea	<i>Balaenoptera borealis</i>	H	→45 M
		<i>Leptonychotes weddelli</i>	Gb	3-29 O

Many species of the different notothenioid families feed on amphipods to a more or less broad range (Table 6.3). Bottom species such as dragonfishes (bathydraconids) and plunderfishes (artetidraconids and harpagiferids) actively prey upon benthic amphipods, sometimes to a very large extent (up to 96% of diet mass). Most of the species that feed in the water column, like icefishes (channichthyids), consume rather few amphipods, mainly hyperiids. Finally, members of the family Nototheniidae (rockcods) show a more complex behaviour, feeding on both benthic and pelagic animals; gammarideans as well as hyperideans are usual preys, forming up to 88% of diet mass in *e.g.* *Notothenia coriiceps*. Beside notothenioids, many other fish families were reported to consume amphipods, the most important one being the myctophids (lanternfishes). These small-sized, meso- or bathypelagic fish prey to a relatively small extent on different hyperidean families but, owing to their abundance and to their peculiar swarming behaviour, maybe represent the largest group of amphipod consumers in the Southern Ocean (see below).

All the Antarctic and Sub-Antarctic seabird families have been reported to feed on (pelagic) amphipods. If the latter constitute only a small fraction in the diet of albatrosses and gulls, they may form up to 30% of diet mass in terns, which forage closer to the shores. Diving and storm petrels (pelecanoidids and oceanitids) feed at a minor extent too on amphipods, except the Wilson's storm petrel (*Oceanites oceanicus*) for which these crustaceans can form up to 45% of food bulk. Most of the procellariids (petrels, prions and shearwaters) also feed occasionally on amphipods which usually constitute less than 5% of their diet mass. Finally, all the Southern Ocean penguins (sphenicids) have been reported to prey on hyperiids and pelagic gammariids, but to a very small extent (about 1% in mass); macaroni penguins (*Eudyptes chrysolophus*), however, seem to feed more frequently on amphipods (up to 67% in mass); typically benthic amphipod species are

also found in the diet of gentoo penguins (*Pygoscelis papua*), denoting that these birds feed near to the shorelines.

Among marine mammals, 10 species—4 baleen whales, 1 dolphin and 5 seals—have been found with amphipods in their stomach. The presence of these crustaceans in the diet of plankton-feeding cetaceans is not surprising as hyperiids like *Themisto gaudichaudii* are known to swim often at the vicinity of krill swarms (Pakhomov & Perissinotto 1996). The sei whale (*Balaenoptera borealis*) in particular seems to feed preferentially on this hyperiid which can form up to 45% of its diet mass (Kawamura 1974), while for the other whales the occurrence of amphipods is more anecdotal. Amphipods are also found in the diet of many Antarctic seal species, where they form only a few ‰ in mass, but most of the authors claim it should be an artifact, amphipods coming from the stomach of ingested fish.

To synthesize the dataset, a tentative 'box-model' was built up which shows the relative importance of both pelagic and benthic amphipods in the diet of the Southern Ocean top predators. To construct this model, various published data were used: (i) the mean quantitative values of amphipod mass fractions in predators' diet, (ii) the standing stocks of the main groups of predators in the Southern Ocean, (iii) the feeding rates of these predators. Available data are presented in Table 4; for some groups, namely both benthic and pelagic (squids) invertebrates, consistent biomass values are lacking, causing the total amount of preyed amphipods to be underestimated. The diagram (Fig. 1) shows the estimates of the different predation fluxes, expressed in millions of tons per year (Mt.yr^{-1}). It clearly appears that pelagic fishes (myctophids) are responsible for the biggest flux (50 Mt.yr^{-1}), which can easily be understood when considering the area and depth ratios of the oceanic vs neritic zones. The second group in importance is represented by benthic and benthopelagic fish (notothenioids mainly), whose predation on pelagic amphipods was not estimated but is likely at least one order of magnitude smaller than on benthic ones (8.6 Mt.yr^{-1}). The other predator groups (birds and mammals) consume

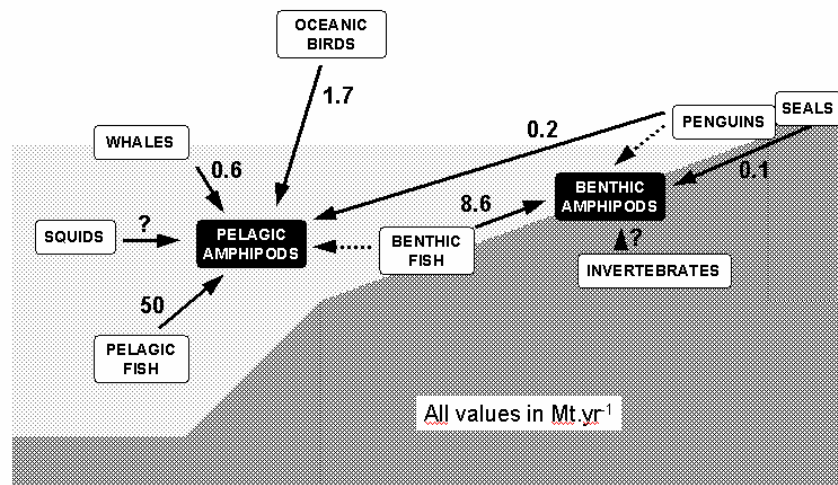
a lower amount of amphipods (from 0.1 to 1.7 Mt.yr⁻¹) as their relative biomass is far weaker than that of fish. The total amphipod mass ingested per year is thus estimated at roughly 60 Mt. These values must however be cautiously regarded as they are tainted with biases and approximations for several reasons: (i) predator biomass data are usually widely scattered, available only either for areas of intensive scientific research or for species of commercial significance; (ii) just a few (characteristic) fish families were taken into account, while other ones (such as *e.g.* zoarcids or muraenolepids) are also well represented in the Southern Ocean but less studied; (iii) seasonal variations in either predator standing stocks or feeding rates are likely to occur, the importance of which can hardly be weighed; (iv) the proportion of amphipods in predators' diet may considerably vary with respect to several parameters like *e.g.* age, sex or geographical location; (v) some maybe significant groups (*i.e.* benthic and pelagic invertebrates) were totally omitted; (vi) the circumscription of what is the 'Southern Ocean' (south of the Antarctic Convergence, south of the Sub-Tropical Front, including or not the Sub-Antarctic islands) is not clearly defined in the literature. This notwithstanding, values presented in Fig. 1 can be considered to represent a rather realistic working hypothesis about the importance of amphipods for Southern Ocean top predators.

Table 6.4: Values of the different parameters used to estimate the predation rates on amphipods by the main Southern Ocean predator groups.

Parameters	Values	References
Southern Ocean Area	37 10 ⁶ km ²	Stonehouse 1989
Continental Shelf Area (Continent)	2 10 ⁶ km ²	
Continental Shelf Area (Islands)	0.5 10 ⁶ km ²	
Demersal Fish Biomass (Continent)	0.9 T.km ⁻²	Kock 1992
Demersal Fish Biomass (Islands)	20 T.km ⁻²	<i>estimated from</i> Kock 1992
Myctophid Biomass	140 MT	Lubimova <i>et al.</i> 1987 in Kock 1992
Fish Mean Daily Ingestion Rate	2 %.day ⁻¹	various authors in Kock 1992
Penguin Annual Ingestion Rate	17 MT.yr ⁻¹	various authors in Williams 1995

Parameters	Values	References
Other Seabirds' Annual Ingestion Rate	35 MT.yr ⁻¹	<i>extrapolated from</i> Croxall & Prince 1987
Sei Whale Antarctic Population	24000 ind.	<i>mean from various sources</i>
Sei Whale Feeding Period	130 days.yr ⁻¹	
Sei Whale Daily Ingestion	900 kg.day ⁻¹	Kawamura 1974
Seal Mean Daily Ingestion Rate	7 kg.km ⁻² .day ⁻¹	Joiris 1991
Amphipods in Diet	Mean (%)	
Demersal Fish (Notothenioids)	10	<i>this study</i>
Pelagic Fish (Myctophids)	5	"
Penguins	1	"
Oceanic Seabirds	5	"
Whales	20	"
Seals	2	"

Fig. 6.1: Scheme of the different predation fluxes on amphipods (in MT.yr⁻¹) by the main Southern Ocean predator groups.



6.3. CONCLUSIONS

The exhaustive analysis of the literature dedicated to the diet of Southern Ocean top predators revealed the importance of amphipods in the trophodynamics of the higher food web. The integration of available data with published values about predators' biomasses and feeding rates allowed to estimate that about 60 millions of tons of these crustaceans are consumed each year in the area, *i.e.* about $1.6 \text{ t.km}^{-2}.\text{yr}^{-1}$. By comparison, the consumption of krill by all its predators in the Southern Ocean has been estimated to about 250 Mt.yr^{-1} (Everson 1977, Miller & Hampton 1989), while annual fish consumption by warm-blooded predators has been estimated to be up to 15 Mt (Everson 1977, Laws 1985). Amphipods are thus likely to be the second group of animal prey in importance after euphausiids. The present review also emphasizes the major role of hyperiids (and especially of *Themisto gaudichaudii*) in Antarctic food webs.

Acknowledgements

The present research was performed under the auspices of the Scientific Research Programme on Antarctic (Phase IV) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC contracts n° A4/36/B02 and EV/36/24A). The authors would like to thank Dr Yves Cherel (Centre d'Etudes Biologiques de Chizé, France) who provided several references used for constructing the dataset, and participants to the VIIIth SCAR Biology Symposium (Amsterdam, August 2000) for fruitful discussions. The second author (F. N.) received a grant from the Belgian "Fonds de la Recherche pour l'Industrie et l'Agriculture" (FRIA). This is MARE publication MARE011.

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CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

The main objective of this work was to assess the ecological role of amphipod crustaceans in the Southern Ocean and more particularly their significance in the benthic trophic webs of the eastern Weddell Sea and the Antarctic Peninsula.

This final chapter is intended to provide:

- (1) an integrated overview of the results detailed in previous chapters, in order to present an overall image of amphipod crustaceans trophic significance and diversity in Antarctic shelf benthic communities. This section will include data obtained for other groups representative of the Antarctic benthos in order to get a global picture of the benthic food webs where amphipods are involved as well as some considerations on benthic-pelagic coupling in the study area,
- (2) an evaluation of the usefulness of stable isotope ratios (in particular, of carbon and nitrogen) and fatty acids as natural trophic biomarkers,
- (3) and finally, the major conclusions drawn from this study.

7.1. TROPHIC SIGNIFICANCE OF AMPHIPOD CRUSTACEANS IN ANTARCTIC BENTHIC COMMUNITIES AND SOME CONSIDERATIONS ABOUT BENTHIC-PELAGIC COUPLING

Until about 20 years ago the main flow of energy in Antarctic marine environment was considered to be a direct food chain from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. Heywood and Whitaker 1984). Those simple food chain descriptions, however, fall quite short of reality (Marchant and Murphy 1994). Indeed, diatoms are major components of Antarctic marine phytoplankton but other production pathways have to be considered as, notably, the microbial loop (e.g. Cota et al. 1990, Sullivan et al. 1990). The sea-ice community also is suspected to be an important food source for some Southern Ocean invertebrates (Marschall 1988, Daly 1990). Considering all those aspects, the Antarctic marine food web is now considered to be as complex as many others in lower-latitude ecosystems (Garrison 1991).

As they may explain part of the apparent discrepancies between seasonally limited food resources and the richness of benthic life, the study of the feeding habits have received considerable attention in the last decades (Arntz et al. 1994). However, because of the large number of benthic and benthopelagic species and the wide and variable food spectra of many of these, there subsist many trophic interactions to clarify. Furthermore, due to the remoteness of the region, research in Antarctica is never an easy task to achieve. Many factors have to be taken into account: the financial costs of all logistics implied by an expedition to the Antarctic as well as the strong seasonality of the Southern Ocean system are some of the parameters that have to be considered.

The reason for focusing this work on amphipod crustaceans can be briefly summarized as follow:

- (i) With more than 830 different species, among which about 75% endemics, the amphipod crustaceans form one of the most speciose animal group of the Southern Ocean (De Broyer & Jazdzewski 1996).
- (ii) These peracarids have colonized a wide variety of ecological niches, in benthic habitats as well as in the water column (De Broyer *et al.* 2001), and have developed a large range of feeding strategies, from suspension-feeding to scavenging on big carrion and specialized modes like micro-predatory browsing on invertebrate colonies (Dauby *et al.* 2001; Nyssen *et al.* 2002).
- (iii) Furthermore, peracarid crustaceans are important food sources for many Southern Ocean benthic invertebrates (see review in chapter VI). Indeed, the discrepancy between the suspected ecological significance of amphipods and our poor knowledge of their eco-functional role calls for a more detailed investigation of their role in Antarctic trophodynamics.

We approached the trophic ecology of amphipods in a multidisciplinary way, but nevertheless methods lead to the same conclusion: amphipod trophic ecology is diverse, rich and complex.

Even, in their morphology, and we have investigated the mandible in particular because of its central role in the nutrition, they appear to have developed a multitude of morphological patterns (see Chapter IV). However, the link between amphipods mandible morphology and feeding habits is often not sufficiently distinct to be considered as a reliable method of trophic classification. The evolution of amphipod mandible morphology has not only been guided by its alimentary functionality, but other factors did interfere also in the process. However, the global analysis of all mouthparts

morphological features (maxillipeds, maxille 1 and maxille 2) would probably provide better insights to infer trophic type.

As demonstrated also by the other approaches considered in this work (stable isotopic ratios and fatty acid composition analyses, see chapters II and III), few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods do. Considerably wide ranges have already been recorded for pelagic amphipod species from the same sampling area (Rau et al. 1991). Therefore, as trophic diversity is generally associated to functional role diversity, both benthic and pelagic amphipods appear as key components in Antarctic systems.

Our data indicate that benthic amphipods live at many trophic levels of the Weddell Sea food web (see chapters II & III). And, besides some highly specialized species as for example, micro-grazers feeding on a single food item (species of the genus *Echiniphimedia* feed exclusively on sponges, as revealed by their guts full of hexactinellid spicules) there are numerous signs of opportunism in amphipod feeding behavior.

The trophic characterization of amphipod based on isotopic values coincides quite well with the trophic classification based on gut contents analyses. So, as the fundamental difference between both approaches to diet studies is the time scale each method addresses – diet integration over weeks for the first and snapshot of last meals for the latter - this similarity indicates that overall there are only small changes in diet over lifetime.

The presence of amphipods at all levels of Weddell Sea benthic food web can be generalized to the other ecosystem considered in this study: the Antarctic Peninsula.

Based on our own unpublished stable isotope data of zoobenthos in Antarctic Peninsula, we can exemplify an Antarctic food web including amphipods to figure out which position they occupy and how important they are among the

other zoobenthic groups. All analyzed organisms are listed in Table 7.1. As chapter III has been conducted in the same area, we can refer to it for the sampling map. Among amphipods, sixteen species have been considered. This collection gathers several feeding types, notably, suspension-feeder (*A. richardsoni*), deposit-feeders (*Byblis* sp., *P. gibber*), micrograzers (*E. echinata*, *E. hodgsoni*, *E. similis*), predator (*Iphimediella* sp.), scavengers (e.g. *A. plebs*, *P. coatsi*, *W. obesa*). We have classified amphipods into hyperids and gammarids because of their different habitats, the hyperid amphipods being exclusively planktonic.

Table 7.1. Carbon and nitrogen isotopic ratios (mean \pm SD, ‰) of all animals sampled on the shelf of the Antarctic Peninsula; TL corresponds to estimated trophic level

PHYLUM	Class / Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL
CNIDARIA	Hydrozoa	-26.9 ± 0.0 (1)	4.9 ± 0.0 (1)	2,9
	Anthozoa	-25.1 ± 1.3 (6)	7.8 ± 0.7 (6)	4,1
	Scyphozoa	-24.1 ± 0.3 (2)	7.7 ± 0.6 (2)	4,0
ANNELIDA	Polynoid	-24.4 ± 0.4 (2)	9.3 ± 0.9 (2)	4,7
	<i>Laetmonice producta</i>	-23.7 ± 0.5 (2)	8.9 ± 1.0 (2)	4,5
MOLLUSCA	Cephalopoda			
	<i>Paraledone turqueti</i>	-24.2 ± 0.4 (7)	9.6 ± 0.7 (7)	4,8
	<i>Paraledone charcoti</i>	-25 ± 0.0 (1)	8.6 ± 1.0 (1)	4,4
	<i>Paraledone</i> sp.	-24.7 ± 0.0 (1)	8.5 ± 0.0 (1)	4,4
	<i>Megaledone setosus</i>	-21.5 ± 0.0 (1)	9.5 ± 0.0 (1)	4,8
	Bivalvia			
	<i>Limopsis marionensis</i>	-24.3 ± 1.6 (5)	7.7 ± 0.8 (5)	4,0
ARTHROPODA	Isopoda			
	<i>Glyptonotus antarcticus</i>	-22.9 ± 0.0 (1)	6.3 ± 0.0 (1)	3,5
	<i>Seratoserolis trilobitoides</i>	-22.9 ± 1.2 (2)	7.5 ± 0.2 (5)	4,0
	<i>Natatolana</i> sp.	-21.6 ± 0.8 (6)	6.8 ± 0.4 (6)	3,7
	Antarcturidae gen. sp	-21.4 ± 1.5 (4)	6.3 ± 0.8 (6)	3,5
	Mysidacea	-26.3 ± 0.0 (1)	4.5 ± 0.0 (1)	2,7
	Amphipoda			
	Hyperid			
	<i>Themisto</i> sp	-25.1 ± 0.7 (2)	2.9 ± 0.7 (2)	2,0
	Gammarid			
	<i>Ampelisca richardsoni</i>	-29.3 ± 0.2 (3)	4.1 ± 0.1 (3)	2,5
	<i>Byblis</i> sp	-24.8 ± 1.2 (3)	6.1 ± 0.3 (3)	3,4
	<i>Eusirus perdentatus</i>	-23.4 ± 0.7 (19)	7.3 ± 1.0 (19)	3,9
	<i>Djerboa furcipes</i>	-27.8 ± 0.6 (5)	4.9 ± 0.3 (5)	2,9
	<i>Echiniphimedia echinata</i>	-21.5 ± 2.1 (3)	6.2 ± 1.0 (3)	3,4
	<i>Echiniphimedia hodgsoni</i>	-24.3 ± 1.3 (2)	10.6 ± 1.8 (2)	5,3
	<i>Iphimediella</i> sp	-21.7 ± 1.0 (6)	11.8 ± 1.0 (6)	5,8
	<i>Pseudorchomene coatsi</i>	-22.7 ± 0.3 (3)	9.3 ± 0.3 (3)	4,7

PHYLUM	Class / Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL
	<i>Waldeckia obesa</i>	-22.8 ± 0.9 (4)	7.3 ± 0.7 (4)	3,9
	<i>Eurythenes gryllus</i>	-27.3 ± 1.1 (9)	8.5 ± 0.5 (9)	4,4
	<i>Abyssorhomene plebs</i>	-26.5 ± 0.4 (6)	9.5 ± 0.8 (6)	4,8
	<i>Epimeria georgiana</i>	-22.9 ± 1.9 (9)	7.9 ± 0.4 (9)	4,1
	<i>Epimeria similis</i>	-25 ± 1.4 (15)	7.6 ± 0.5 (15)	4,0
	<i>Leucothoe spinicarpa</i>	-22.7 ± 0.6 (6)	8.3 ± 0.8 (6)	4,3
	<i>Paraceradocus gibber</i>	-23.5 ± 0.7 (12)	5.0 ± 0.5 (12)	2,9
	Euphausiacea			
	<i>Euphausia superba</i>	-28.6 ± 1.1 (6)	2.8 ± 0.4 (6)	2,0
	Decapoda			
	<i>Notocrangon antarcticus</i>	-23.6 ± 0.3 (4)	9.3 ± 0.2 (4)	4,7
	<i>Chorismus antarcticus</i>	-24.0 ± 1.8 (2)	7.4 ± 1.3 (2)	3,9
BRYOZOA	<i>Reteporella</i> sp.	-26.9 ± 0.0 (1)	6.5 ± 0.0 (1)	3,5
ECHINODERMATA	Crinoidea	-26.1 ± 0.0 (1)	7.9 ± 0.0 (1)	4,1
	Holothuroidea			
	<i>Psolus</i> sp.	-26.6 ± 1.4 (3)	8.0 ± 0.8 (3)	4,2
	<i>Bathyploes fusciculum</i>	-24.8 ± 0.3 (2)	8.8 ± 0.7 (2)	4,5
	<i>Echinocucumis</i> sp.	-29 ± 0.3 (2)	7.5 ± 0.2 (2)	4,0
	Ophiuroidea			
	<i>Astrotoma agassizii</i>	-23.9 ± 2.1 (3)	7.5 ± 0.9 (3)	4,0
	<i>Ophioparte gigas</i>	-27.3 ± 1.6 (3)	5.5 ± 0.4 (3)	3,1
	<i>Ophionotus</i> sp.	-24.5 ± 1.5 (2)	6.7 ± 0.2 (2)	3,6
	Asteroidea	-24.0 ± 1.6 (4)	11.2 ± 1.3 (5)	5,5
CHORDATA	Osteichthyes			
	Channichthyidae			
	<i>Champscephalus gunnari</i>	-25.1 ± 0.3 (5)	8.5 ± 0.3 (5)	4,4
	Nototheniidae			
	<i>Gobionotothen gibberifrons</i>	-24.3 ± 0.1 (5)	9.8 ± 0.4 (5)	4,9
	<i>Notothenia coriiceps</i>	-23.6 ± 0.8 (6)	9.9 ± 0.6 (6)	5,0
	<i>Notothenia rossii</i>	-24.4 ± 0.5 (6)	9.2 ± 0.3 (6)	4,7
	<i>Trematomus bernacchii</i>	-19.7 ± 2.0 (2)	12.6 ± 0.2 (2)	6,1
	<i>Trematomus pennellii</i>	-20.2 ± 0.6 (3)	11.0 ± 0.8 (3)	5,4
	<i>Trematomus nicolaii</i>	-20.5 ± 0.0 (1)	11.0 ± 0.0 (1)	5,4
	<i>Trematomus hansonii</i>	-21.9 ± 0.0 (1)	10.2 ± 0.0 (1)	5,1
	<i>Trematomus eulepidotus</i>	-24.5 ± 0.4 (5)	9.0 ± 0.6 (5)	4,6

As observed in the figure 7.1., the most striking features are, on the one hand, a general impoverishment in ^{13}C compared to other systems (e.g. tropical), probably originating from a depleted food source but transferred throughout the food web. This pronounced depletion in ^{13}C at the base of Antarctic food web is not new. The SPOM isotopic ratios are considerably lower than values previously recorded for other regions but within the range of Antarctic as well as Arctic values (Wada et al. 1987, Hobson et al. 1995, Dunton 2001, Corbisier et al. 2004). Polar SPOM is in general depleted in ^{13}C as compared with predominantly

temperate SPOM ($-22 \pm 3\text{‰}$) (reviews in Rau et al. 1982, Fischer 1991, France 1995). Low temperature (below 2°C), low light intensity and high water $[\text{CO}_2(\text{aq})]$ values lead to very low ^{13}C content in the phytoplankton (Rau et al. 1989, 1991a). Thompson and Calvert (1994) also suggest a substantial role of irradiance in process of ^{13}C incorporation in marine diatoms.

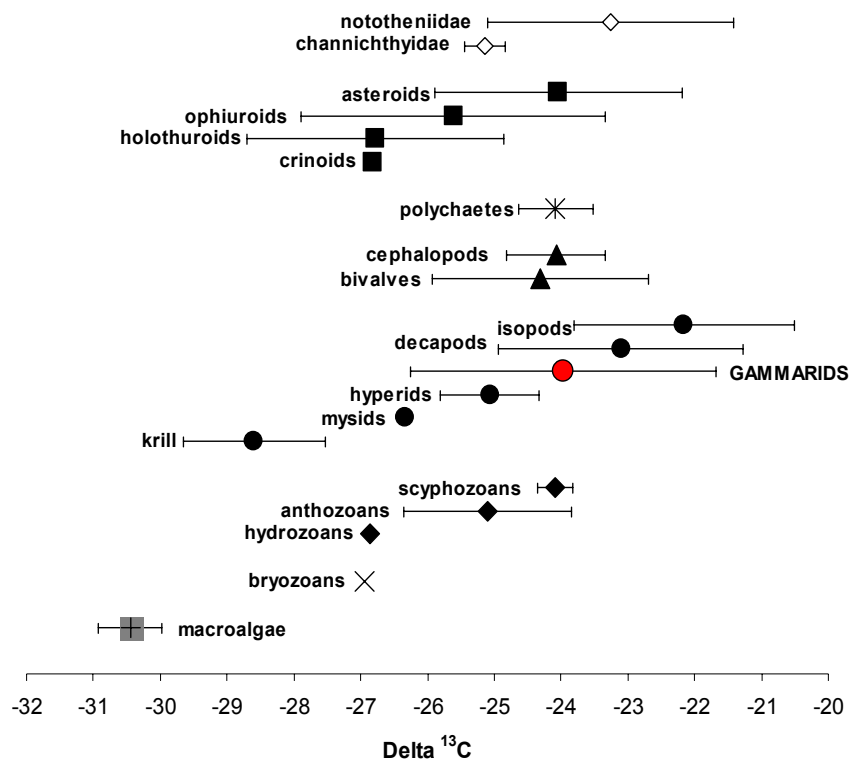
On the other hand, a considerable overlap of the $\delta^{13}\text{C}$ values is observed between groups.

The carbon isotopic signature of euphausiids (-28.6‰) corresponds to the range of particulate organic matter that is derived from phytoplankton (-30.4 to -28.0‰ ; Fisher 1991, Rau et al. 1991, Fisher & Wiencke 1992). Other invertebrates that demonstrated a clear dependence on phytoplankton (based on $\delta^{13}\text{C}$ values) included bryozoans, hydrozoans, holothurians, crinoids, mysids and some amphipods.

Studies of high latitude marine food webs suggest that stable carbon isotope analysis may be useful in elucidating the degree to which benthic consumers are coupled to pelagic primary production (McConnaughey & McRoy 1979, Dunton et al. 1989, Hobson et al. 1995). Close coupling of consumers with pelagic primary production results in less ^{13}C enrichment in consumer tissues compared with these links in deposit feeders and detrital-based food webs.

Our isotopic investigations support the hypothesis that a major part of the benthic community is supported primarily by phytoplanktonic POM reaching the benthos. Carbon evidence for this is the similarity in $\delta^{13}\text{C}$ values between pelagic POM-based feeders (e.g. *Euphausia superba*, *Themisto* sp.) and benthic filter feeders (e.g. *Echinocucumis* sp., *Ampelisca richardsoni*); (Table 7.1., Fig. 7.1.). Similar results have been found in isotopic investigations of Arctic marine food webs (Dunton et al. 1989, Hobson et al. 1995). Benthic organisms in systems exhibiting weaker benthic-pelagic coupling would be expected to be substantially enriched in ^{13}C relative to both POM and POM grazers.

Fig. 7.1. Distribution of stable-carbon isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula



In our study, the possible sources of significant primary production were POM, macroalgae and ice algae. The coastal waters along the west side of the Antarctic Peninsula and nearby islands are characterized by a rich and dense macroalgal flora composed of annual and perennial species (Zielinski 1990, Chung et al. 1994, Klöser et al. 1994, Amsler et al. 1998). Large amounts of algae are degraded, so they become a suitable food resource for benthic organisms (Richardson 1979, Brouwer 1996, Iken et al. 1997, 1998). Detached algae can be decomposed by biological and hydrodynamical processes (Reichardt & Dieckmann 1985, Rakusa-Suszczewski 1993) and

some may drift into deeper waters to provide food for benthic deposit and suspension feeders (Fischer & Wiencke 1992). The macroalgae $\delta^{13}\text{C}$ values we have recorded range from -31 to -30‰. Owing to the strong similarity with POM isotopic ratios (see Chapter II, Nyssen et al. 2002), it was impossible to distinguish between these two primary producers on a carbon isotopic base. On the contrary, the difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between SPOM and ice algae, generally more enriched (e.g. $\delta^{13}\text{C} = -18.5\text{‰}$, $\delta^{15}\text{N} = 8.3\text{‰}$, Hobson et al. 1995) (Fischer et al. 1991, Rau et al. 1991, Kennedy et al. 2002) permit further insight into the relative input of these sources to the food web. While the enrichment in ^{13}C from POM to some POM grazers may point towards some contribution of ice algae, $\delta^{15}\text{N}$ values clearly indicate direct feeding on POM and not on the isotopically heavier ice algae. Low $\delta^{13}\text{C}$ values were generally maintained through the food web, including fishes and benthic invertebrates, again confirming the importance of POM as a major food source for the entire food web. It has to be mentioned that those conclusions are based on isotopic ratios only and then, the contribution of macroalgae as a primary carbon source in the food web can not be totally excluded (see section 7.2.).

From the nitrogen stable isotopic ratios of euphausiids (2.8‰) and the mean value of 0.4‰ used by Dunton (2001) for Antarctic phytoplankton, a "per-trophic-level" ^{15}N enrichment factor of about 2.4‰ was applied to obtain trophic level estimates according to the relationship:

$$TL = (D - 0.4)/2.4 + 1$$

Where D is the $\delta^{15}\text{N}$ value of the organism, 0.4 refers to the mean value of SPOM, and TL is the organism's trophic level.

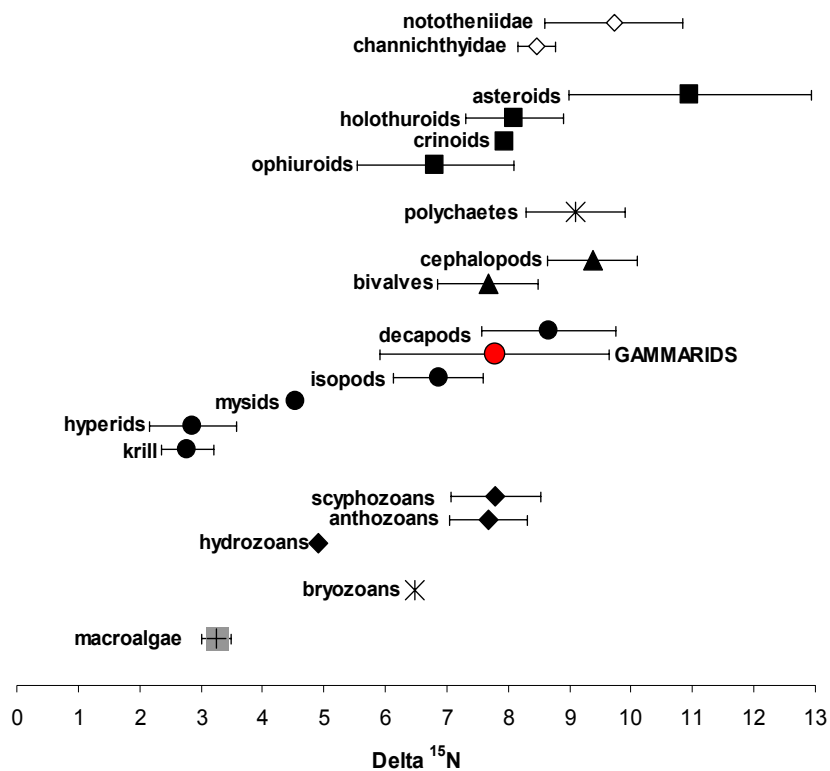
Based on the assumption that POM is the first trophic level, the range of $\delta^{15}\text{N}$ values in Antarctic Peninsula fauna reflects a food web characterized by 6 trophic levels, the highest level being occupied only by the demersal emerald

rockcod *Trematomus bernachii*. Other Fish range over two trophic levels from planktivorous species such *Champsocephalus gunnari* and *Trematomus eulepidotus* (TL 4.4 to 4.6) through *Trematomus pennellii* and *T. nicolai* (TL 5.4), which are predatory on larger benthic invertebrates and fishes (Gon and Heemstra 1990, Barrera-Oro 2002). They share these levels of the food web (4th and 5th ones) with asteroids, cephalopods, polychaetes and some amphipod and decapod crustaceans (see Fig. 7.2.). The sixteen species of amphipods considered in this study range over 3 trophic levels from herbivorous species (*A. richardsoni*, *D. furcipes*, TL 2.5 and 2.9, respectively) to scavengers (*E. gryllus*, *A. plebs*, TL 4.4 to 4.8) and predator (*Iphimediella* sp, TL 5.8). One can be surprised by the trophic levels estimation which put species between two consecutive trophic levels. Those calculations have to be considered with caution. Indeed, as they are based on assumptions (SPOM isotopic ratio, exclusive trophic link between SPOM and krill ...), one can suppose that are probably biased. Those trophic level estimations then provide only a rough idea of each group relative position in the food web.

Among amphipods in general, the trophic relationships predicted by $\delta^{15}\text{N}$ are in good agreement with information in the literature and with results we obtained previously (see Chapter II and III; Nyssen et al. 2002, Nyssen et al. 2005). For example, the well established trophic link between the species *Epimeria similis* and hydrozoans is confirmed by their carbon and nitrogen isotopic ratios (see Table 7.1.). However, for species such as the iphimediids *Echiniphimedia echinata* and *E. hodgsoni*, some clarifications are needed. Although gut contents indicate an exclusive reliance on sponges for both species, their carbon and nitrogen isotopic ratios differ respectively by 3‰ and 4‰, resulting in a difference of 2 trophic levels between them. This can be due to the consumption of different sponge species, as wide range of isotopic ratios have been recorded for these sessile organisms during this study ($\delta^{13}\text{C}=-26.5$ to -23.2 ‰ and $\delta^{15}\text{N}=3.9$ to 9.9 ‰ (Nyssen, unpublished

data). These isotopic values are also coherent with the classification of another amphipod species, *Leucothoe spinicarpa* ($\delta^{13}\text{C} = -22.7 \pm 0.6\text{‰}$ and $\delta^{15}\text{N} = 8.3 \pm 0.8\text{‰}$) as sponges consumers. This species is known to live in sponge atrial cavities as well as in ascidians (Thiel, 1999, personal observations).

Fig. 7.2. Distribution of stable-nitrogen isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula



The results of this analysis confirmed known trophic relationships among Peninsula organisms and revealed their position in the food web (Table 7.1).

The analysis also demonstrated that many consumers occupy similar trophic levels, but derive their carbon from different sources. For example, as first level consumers, both amphipods species *A. richardsoni*, *P. gibber* have similar $\delta^{15}\text{N}$ values (4.1‰ – 5.0‰), but their $\delta^{13}\text{C}$ values differ by 6‰ suggesting different carbon sources. Revealed as deposit-feeder from gut content analyses, *P. gibber* derives probably its carbon from microbially reworked organic matter that forms a thin layer on the sediment, whereas *A. richardsoni* feeds exclusively on phytoplankton (Dauby et al. 2001, Nyssen et al. 2002, Nyssen et al. 2005).

7.2. AN EVALUATION OF THE EFFICIENCY OF STABLE ISOTOPES AND FATTY ACIDS AS NATURAL TROPHIC BIOMARKERS

Stable carbon isotopes can be powerful tracers of the sources of organic carbon sustaining consumer communities, provided that the primary carbon sources are adequately characterized and differ in their $\delta^{13}\text{C}$ signatures (reviewed by Lajtha & Michener 1994). The latter conditions are essential; however, unfortunately, they are not always met. Furthermore, phytoplankton is a difficult component to characterize isotopically, as it is practically infeasible to separate it from the detrital suspended matter pool. Its carbon isotope composition is thus often masked and the available value corresponds to a mixing of the different components.

Stable isotopes of nitrogen usually have little value as an indicator of the primary nitrogen sources of a consumer's diet, but have proven to be an indicator of the trophic level of organisms, due to the more pronounced fractionation that occurs between trophic levels. However, drawbacks in its application remain that (i) the degree of fractionation shows a rather large variability and may be dependent on the N content of the food source (as an indicator of the food quality) (Adams & Sterner 2000), and (ii) that the mechanisms underlying the fractionation of ^{15}N are still poorly understood (see Chapter I for a more thorough discussion). Therefore when detailed information on the trophic position of an organism is required, it may be necessary to determine the actual degree of fractionation under controlled conditions first (Hobson et al. 1996, Gannes et al. 1997, Webb et al. 1998, Gorokhova & Hansson 1999). Fortunately, in many cases, such detailed information is not required, and (average) $\delta^{15}\text{N}$ data of consumers can still provide very useful information.

During our study, we experienced directly one of the weak points inherent to stable isotope analysis. In the Antarctic Peninsula, we had the opportunity to

sample the brown macroalgae *Desmarestia menziesii*. Usually, isotopic distinction between phytoplankton and macroalgae is quite obvious, but our brown macroalgae samples were highly depleted in carbon compared to the data referred by other authors for Antarctic Peninsula (Dunton 2001, $\delta^{13}\text{C}$ values of five common species of large brown algae ranged from -14 to -25‰, Corbisier et al. 2004). In this case, the estimation of each primary producer contribution to consumers' diet was very difficult. To counteract inconveniences inherent to a technique, one solution is to combine it with another one, so that the new dimension brought by the second method can make up for the lacks of the initial method.

The combined use of stable isotopes and fatty acids as trophic biomarkers has effectively facilitated the understanding of the trophic relationships between the different organisms in Antarctic ecosystems. Indeed, we were not able to separate different primary producers (phytoplankton and macroalgae) based on their carbon isotopic signatures, but based on their distinct fatty acid composition. Thus, the presence or absence in consumers of fatty acid biomarkers of phytoplankton or of macroalgae has allowed assessing the contribution of each primary producer to higher trophic levels. For example, from their similar isotopic values, the amphipod species *A. richardsoni* and *D. furcipes* were both classified as primary consumers. Their respective fatty acid profiles reveal that, even if they were at the same trophic level, they did not rely on the same primary producers: the former being a suspension-feeder and the latter a macroalgae consumer. On the other hand, isotopic data did assist in the correct interpretation of fatty acid compositions, too. As illustrated in Chapter III, significant proportions of monounsaturated fatty acids typical of dominant Antarctic copepods (Hagen et al. 1993, Kattner et al. 1994, Hagen et al. 2000) in the amphipod *Iphimediella* sp. would have classified this species as a zooplankton feeder. However, its $\delta^{15}\text{N}$ value (highest value for amphipod

ever recorded so far in Antarctic, to our knowledge) as well as its known predatory behaviour strongly indicates that there exists an additional trophic level between copepods and *Iphimediella* sp.

So, the combination of fatty acid trophic markers and stable isotope analyses may provide additional information for resolving trophic interactions in marine ecosystems.

7.3. CONCLUSIONS

Recent reviews on the knowledge about marine biodiversity in the Southern Ocean (e.g. Arntz et al. 1997) have stressed for instance the relative importance of some zoological groups, like mollusks and polychaetes, and the predominance of crustaceans. Among the latter, amphipods form the most diversified group within the Antarctic macrozoobenthos, both from the taxonomic point of view (more than 830 species have been recorded in the Southern Ocean (De Broyer and Jazdzewski 1996) as by niche occupation (De Broyer et al. 2001, Dauby et al. 2001) and at the community level.

The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their share in Antarctic trophodynamics as well as a more systematic and efficient approach towards this aspect of their ecology.

Our multidisciplinary approach has allowed tackling the complex problem of amphipod trophic role in the Southern Ocean from different angles, each adding a particular aspect to overall food web picture.

All along this study, we have completed the gut content data base and have widened the impressive trophic spectrum suspected for the Antarctic amphipods. Although the numerous biases brought by gut content analyses, they are still essential to obtain a rough pre-classification of species in different trophic types. The revealed trophic categories are numerous and diversified, from the typical suspension feeders to the obligate scavengers. If a lot of species are opportunist, some amphipods have been revealed as very specialized in food foraging, sometimes pushing the selection to mono-specific level. In general, these first categorizations achieved with gut contents were globally confirmed afterwards by the analytical methods.

Part of this work has revealed that the degree of specialization reached sometimes in the food selection is unfortunately not reflected by the morphology, at least not enough to lead to an indisputable conclusion. We have to remind that we did only consider morphology of mandible because of its crucial role in the feeding. But the examination of the other mouthparts to get a more global idea of the functioning would probably enhance the accuracy of the conclusions.

We have also demonstrated that both fatty acid composition and stable isotope ratios are suitable tools for trophic ecosystem analysis in their own right. Fatty acids point towards food web links and stable isotopes identify trophic positions. However, the use of only one of the two tools can sometimes lead to misinterpretations with serious implications. The combination of both the approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution. In the same line, another interesting approach that could be used in the future to characterize carbon fluxes between prey and predators as well as to validate the applicability of both methods, involves feeding experiments with ^{13}C -enriched experimental diets. Such studies would provide informations on carbon accumulation, transfer and turnover rates as well as biosynthesis of lipids and individual FA (e.g. Albers 1999).

Another aspect of amphipod trophic ecology that could be worth to consider in future researches is the contribution of bacteria to their diet. Bacteria influence undoubtedly Antarctic invertebrates feeding and more particularly the species such as the deposit-feeders which feed on the thin layer covering sea bottoms.

During this study, we have often been confronted to the scavenger trophic guild, essentially constituted by species of the Lysianassoidea super family. The trophic link between the pelagic and benthic scavenger assemblages formed by large food falls has been understudied in marine ecological and

carbon/energy cycling research, despite its potentially great significance in marine systems, especially at greater depths.

A potential research could investigate this question in a systematic and synoptic manner by:

- analyzing scavenger food sources with state-of-the-art methods (stable isotopes and fatty acids),
- estimating scavenger energy budgets and food demand,
- using the Antarctic shelf system as a proxy for other marine and especially deep sea systems, which are much more difficult to access.

By evaluating the trophic level of benthic deep-sea communities, but also by determining trophic links they have built with other organisms within this ecosystem, it could be possible to predict how the different compartments of the food web will react to any changes in food supply, natural and/or human-induced.

If the food falls – scavenger link proves to be as important as existing evidence indicates, then the proposed study would alter significantly our view of vertical organic matter/energy transfer in the sea. Furthermore, the results obtained within this work together with information from the literature could be integrated in a balanced model of scavenger assemblage trophic links and energy flows. By outlining the share of scavengers in overall benthic energy flow, this model would show how sensitive the system may be to changes in food supply, i.e. would allow us to estimate how sensible the amount, the frequency and the quality of food falls are to eventual changes (climatic, human-induced) in pelagic ecosystems.

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ANNEX 1: BIODIVERSITY OF THE SOUTHERN OCEAN: A CATALOGUE OF THE AMPHIPODA

From a combination of the checklist of De Broyer C & Jazdzewski K (1993) and the catalogue of Lowry J & Bullock (1976)

BIODIVERSITY OF THE SOUTHERN OCEAN:

A CATALOGUE OF THE AMPHIPODA

(CRUSTACEA)

Combination of De Broyer & Jazdzewski 1993 checklist & Lowry & Bullock
1976 catalogue
+ corrections, update and complements.

Restricted to Gammaridea and Corophiidea (sensu Myers & Lowry, 2003).

Based on a complete survey of taxonomic literature to 31 Dec 2002.
“Ecological” literature may not be complete.

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I. SUB-ORDER GAMMARIDEA

AMPELISCIDAE

- Ampelisca antarctica* Ren, 1991
Ampelisca anversensis Karaman, 1975e
Ampelisca barnardi Nicholls, 1938
Ampelisca bransfieldi K.H. Barnard, 1932
Ampelisca composita Schellenberg, 1931a
Ampelisca dallenei Bellan-Santini, 1985a
Ampelisca dentifera Schellenberg, 1931a
Ampelisca gracilicauda Schellenberg, 1931a
Ampelisca hemicyptops K.H. Barnard, 1930
Ampelisca macrodonta Goeke, 1987
Ampelisca richardsoni Karaman, 1975e
Ampelisca statenensis K.H. Barnard, 1932
Byblis antarctica Schellenberg, 1931a
Byblis securiger (K.H. Barnard, 1931a)
Byblis subantarctica Schellenberg, 1931a
Byblisoides juxtacornis K.H. Barnard, 1931a

AMPHILOCHIDAE

- Amphilochella simplicarpa* Schellenberg, 1926a
Amphilochus marionis Stebbing, 1888
Gitanopsilis amissio Rauschert, 1994
Gitanopsis denticulata Rauschert, 1994
Gitanopsis fucatosquamosa Rauschert, 1994
Gitanopsis inaequipis Schellenberg, 1926a

Gitanopsis pusilla K.H. Barnard, 1916
Gitanopsis simplex Schellenberg, 1926a
Gitanopsis squamosa (Thomson, 1880a)

ASTYRIDAE

Astyra antarctica. Andres, 1997
Eclysis similis K.H. Barnard, 1932

CARDENIOIDAE

CHEIDAE

Cheus annae Thurston, 1982

CLARENCIIDAE

Clarencia chelata K.H. Barnard, 1931a

COLOMASTIGIDAE

Colomastix castellata K.H. Barnard, 1932
Colomastix fissilingua Schellenberg, 1926a
Colomastix simplicicauda Nicholls, 1938
Colomastix sp. 1 Holman & Watling, 1983b

CYPROIDEIDAE

Victorhensenoides arntzi Rauschert, 1996

DEXAMINIDAE

- Atylus dentatus* (Schellenberg, 1931a)
Atylus villosus Bate, 1862
Paradexamine fissicauda Chevreux, 1906b
Paradexamine nana Stebbing, 1914b
Paradexamine pacifica (Thomson, 1879b)
Paradexamine sexdentata Schellenberg, 1931a
Polycheria acanthocephala Schellenberg, 1931a
Polycheria acanthopoda Thurston, 1974b
Polycheria antarctica (Stebbing, 1875b) s.s.
Polycheria cristata Schellenberg, 1931a
Polycheria dentata Schellenberg, 1931a
Polycheria gracilipes Schellenberg, 1931a
Polycheria intermedia Stephensen, 1947a
Polycheria kergueleni (Stebbing, 1888)
Polycheria macrophtalma Schellenberg, 1931a
Polycheria nuda Holman & Watling, 1983b
Polycheria similis Schellenberg, 1931a

DIDYMOCHELIIDAE

- Didymochelia edwardi* Bellan-Santini & Ledoyer, 1987
Didymochelia spongicola K.H. Barnard, 1931a

EOPHLIANTIDAE

- Cylindryllioides mawsoni* Nicholls, 1938
Wandelia crassipes Chevreux, 1906d

EUSIROIDEA

[Bousfield, 1982b, emended; Bousfield & Hendrycks 1997]

EUSIROIDEA : CALLIOPIIDAE

[Bushueva, (1986)] [Bousfield & Hendrycks 1997]

[genera according to Lowry unpubl. list (1998)]

- Atylopsis emarginatus* Stebbing, 1888
Atylopsis fragilis Rauschert, 1989
Atylopsis orthodactyla Thurston, 1974b
?Atylopsis procera Andres, 1986
Calliopiurus excellens Bushueva, 1986
Gondogeneia antarctica (Chevreux, 1906b)
Gondogeneia bidentata (Stephensen, 1927e)
Gondogeneia chosroides (Nicholls, 1938)
Gondogeneia georgiana (Pfeffer, 1888)
South Shetland Islands: King George Island, Admiralty Bay (KJ *et al.* 99).
Gondogeneia gracilicauda (Schellenberg, 1931a)
Gondogeneia macrodon (Schellenberg, 1931a)
Gondogeneia patagonica Alonso, 1986a
Gondogeneia redfearni (Thurston, 1974a)
Gondogeneia simplex (Dana, 1852a)
Gondogeneia spinicoxa Bellan-Santini & Ledoyer, 1974
Gondogeneia subantarctica (Stephensen, 1938c)
Gondogeneia tristanensis (K.H. Barnard, 1932)
Gondogeneia ushuaiae (Schellenberg, 1931a)
Gondogeneia sp. 1 (Stephensen, 1938c)
Gondogeneia sp. 2 (Stephensen, 1938c)
Gondogeneia sp. 3 (Ruffo, 1949)

Gondogeneia sp. 4 J.L. Barnard, 1972b
Gondogeneia sp. 5 Castellanos, 1973
Gondogeneia sp. (= *G. antarctica* cf) [see BK91]
?Haliragoides australis Chilton, 1912a
Harpinioides drepanocheir Stebbing, 1888
Harpinioides fissicauda Schellenberg, 1926a
Lopyastis multisetosa (Schellenberg, 1926a)
Lopyastis signiensis (Thurston, 1974a)
Metaleptamphopus pectinatus Chevreux, 1912a
Oradarea acuminata Thurston, 1974a
Oradarea bidentata K.H. Barnard, 1932
Oradarea crenelata Alonso de Pina, 1995
Oradarea edentata K.H. Barnard, 1932
Oradarea impressicauda K.H. Barnard, 1932
Oradarea megalops (Nicholls, 1938)
Oradarea novaezealandiae (Thomson, 1879b)
Campbell Island: Perseverance Harbour (KS 38c).
Oradarea ocellata Thurston, 1974a
Oradarea rossi Thurston 1974a
Oradarea tricarinata K.H. Barnard, 1932
Oradarea tridentata K.H. Barnard, 1932
Oradarea unidentata Thurston, 1974a
Oradarea walkeri Shoemaker, 1930a
Tylosapis dentata (Stebbing, 1888)

EUSIROIDEA : EUSIRIDAE S.S.

(sensu Bousfield & Hendrycks 1995)

[generic composition according to Bousfield & Hendrycks 1995]

Cleonardo longipes Stebbing, 1888

Cleonardo macrocephala Birstein & Vinogradov, 1955

Eusirella flagella Andres, 1982

Eusiroides aberrantis Bellan-Santini & Ledoyer, 1987

Eusiroides crassi Stebbing, 1888

Eusiroides georgiana K.H. Barnard, 1932

Eusiroides monoculoides (Haswell, 1879)

Eusiroides stenopleura K.H. Barnard, 1932

Eusirus antarcticus Thomson, 1880a *s.l.*

Eusirus bouvieri Chevreux, 1911c

Eusirus giganteus Andres, Lörz & Brandt, 2002.

Eusirus laevis Walker, 1903a

Eusirus laticarpus Chevreux, 1906e

Eusirus microps Walker, 1906c

Eusirus perdentatus Chevreux, 1912a

Eusirus propeperdentatus Andres, 1979b

Eusirus n. sp. 1 De Broyer & Jazdzewski

Eusirus n. sp. 2 De Broyer & Jazdzewski [AV]

Eusirus sp. 3 Puddicombe & Johnstone, 1988

Meteusiroides curvidactyla (Pirlot, 1934)

Rhachotropis anoculata J.L. Barnard, 1962d

Rhachotropis antarctica K.H. Barnard, 1932

Rhachotropis hunteri Nicholls, 1938

Rhachotropis kergueleni Stebbing, 1888

Rhachotropis schellenbergi Andres, 1982

Stenopleura atlantica Stebbing, 1888

EUSIROIDEA : GAMMARELLIDAE

[Bousfield, 1977: 309; Barnard J.L., 1989: 701-703. See also Bnd & Bnd, 1983: 594]

Austroregia batei (Cunningham, 1871)
Austroregia huxleyana (Bate, 1862)
Austroregia Regis (Stebbing, 1914b)
Chosroes decoratus K.H. Barnard, 1932
Chosroes incisus Stebbing, 1888

EUSIROIDEA: PONTOGENEIIDAE

Antarctogeneia macrodactyla Thurston, 1974b
Atyloella dentata K.H. Barnard, 1932
Atyloella magellanica (Stebbing, 1888)
Atyloella quadridens (K.H. Barnard, 1930)
Bovallia gigantea Pfeffer, 1888
Bovallia sp. 1 Monod, 1926
Djerboa furcipes Chevreux, 1906e
Liouvillea oculata Chevreux, 1912a
Paramoera aucklandica (Walker, 1908)

Paramoera brachyura Schellenberg, 1931a
Paramoera chevreuxi (Stephensen, 1927e)
Paramoera edouardi Schellenberg, 1929c
Paramoera fasciculata (Thomson, 1880a)
Paramoera fissicauda (Dana, 1852a)
Paramoera gregaria (Pfeffer, 1888)
Paramoera hamiltoni Nicholls, 1938
Paramoera hermitensis K.H. Barnard, 1932
Paramoera hurleyi Thurston, 1974a

Paramoera husvikensis Thurston, 1974b
Paramoera impressicauda
?Paramoera incognita Bushueva, 1986
Paramoera kergueleni Bellan-Santini & Ledoyer, 1974
Paramoera macquariae Nicholls, 1938
Paramoera obliquimana K.H. Barnard, 1932
Paramoera parva Ruffo, 1949
?Paramoera pfefferi Schellenberg, 1931a
Paramoera schellenbergi Nicholls, 1938
Paramoera tristanensis K.H. Barnard, 1932
Paramoera walkeri (Stebbing, 1906)
Paramoera sp. 1 Shoemaker, 1945d
Paramoera sp. 2 J.L. Barnard, 1972c
Paramoera sp. 3 Bellan-Santini & Ledoyer, 1974 [AV *kergueleni*]
Paramoera sp. 4 Nicholls, 1938
Paramoera spp. Barnard & Karaman, 1991
Pontogeneoides abyssi Nicholls, 1938
Pontogeneoides dubia Ruffo, 1949
Prostebbingia brevicornis (Chevreux, 1906c)
Prostebbingia gracilis (Chevreux, 1912a)
Prostebbingia laevis (Thomson, 1879a)
Prostebbingia longicornis (Chevreux, 1906e)
Prostebbingia serrata Schellenberg, 1926a
Prostebbingia spinicauda Ren & Huang, 1991
Schraderia acuticauda Bellan-Santini & Ledoyer, 1974
Schraderia barnardi Thurston, 1974a
Schraderia dubia Thurston, 1974a
Schraderia gracilis Pfeffer, 1888
Schraderia serraticauda (Stebbing, 1888)
Schraderia sp.1 Castellanos, 1973

[AV] *Frigora ascidicola* Ren, 1991

EXOEDICEROTIDAE

Bathyporeiapus magellanicus Schellenberg, 1931a

Exoediceropsis affinis Alonso de Pina, 1997

Exoediceropsis chiltoni Schellenberg, 1931a

Exoediceropsis lobata Alonso de Pina, 1997

Methalimедon nordenskjoldi Schellenberg, 1931a

Metoedicerops fuegiensis Schellenberg, 1931a

Parhalimедon turqueti Chevreux, 1906b

HADZIOID GROUP

HADZIOID GROUP: CERADOCOPSID GROUP

[Ceradocopsids see Barnard & Barnard, 1983: 635]

Ceradocopsis carnleyi (Stephensen, 1927e)

Ceradocopsis kergueleni Schellenberg, 1926a

Ceradocopsis macracantha Lowry & Fenwick, 1983

Ceradocopsis peke J.L. Barnard, 1972b

Ceradocopsis tristanensis Stephensen, 1949

HADZIOID GROUP: CERADOCID GROUP

[generic composition fide Lowry, unpubl. (1998)]

[see also Ceradocid Group with different composition in Barnard & Barnard,
1983: 373, 612]

Ceradocoides chiltoni Nicholls, 1938

Elasmopus bollonsi Chilton, 1915

Elasmopus neglectus Chilton, 1915
Elasmopus wahine J.L. Barnard, 1972b
Maera incerta Chilton, 1883
Maera mastersi (Haswell, 1880a)
Zygomaera eugeniae (Schellenberg, 1931a)
Zygomaera pfefferi (K.H. Barnard, 1932)
Paraceradocus gibber Andres, 1984
Paraceradocus miersi (Pfeffer, 1888)
Paraceradocus procerus Andres, 1984
Paraceradocus ramulus Andres, 1981
Paraceradocus stenepimerus Andres, 1984
Paraceradocus trispinosus Andres, 1984

HADZIOID GROUP: GAMMARELLA GROUP

Gammarella hybophora Lowry & Fenwick, 1983

HADZIOID GROUP: HADZIIDAE

[Barnard & Barnard, 1983: 651]

Zhadia subantarctica Lowry & Fenwick, 1983

HADZIOID GROUP: MELITIDAE

[Bousfield, 1982b: 281; In Barnard & Barnard, 1983: 662, only *Melita* in MELI]

Melita inaequistylis Dana, 1852a
Melita palmata (Montagu, 1804)
Melita tristanensis K.H. Barnard, 1965
Tagua aporema Lowry & Fenwick, 1983

HADZIOID GROUP: PARAPHERUSA GROUP

Parapherusa crassipes Haswell, 1879b

HADZIOID GROUP: HOHO

Hoho hirtipalma Lowry & Fenwick, 1983

HYALIDAE

Hyale campbellica (Filhol, 1885a)

Hyale grandicornis (Kroyer, 1845)

Hyale hirtipalma (Dana, 1852a)

Hyale macrodactyla Stebbing, 1899

Hyale media (Dana, 1853)

Hyale tristanensis Macnae, 1953

HYPERIOPSIDAE

Hyperopsis australis Walker, 1906a

Hyperopsis sp. Birstein & Vinogradov, 1962b

IPHIMEDIOIDEA

IPHIMEDIOIDEA : ACANTHONOTOZOMELLIDAE

[acc. to Coleman & Barnard, 1991b: 257-258]

[includes Vicmusiidae]

- Acanthonotozomella alata* Schellenberg, 1926a
Acanthonotozomella barnardi Watling & Holman, 1980
Acanthonotozomella rauscherti Coleman & Jäger, 2001
Acanthonotozomella trispinosa (Bellan-Santini, 1972a)
Acanthonotozomoides oatesi (K.H. Barnard, 1930)
Acanthonotozomoides sublitoralis Schellenberg, 1931a
Acanthonotozomopsis pushkini (Bushueva, 1978)

IPHIMEDIOIDEA: AMATHILLOPSIDAE

- Amathillopsis charlottae* Coleman, 1998

IPHIMEDIOIDEA : EPIMERIIDAE

[Coleman & Barnard, 1991b: 255 ([in IPHI in B & K 91))]

- Actinacanthus tricarinatus* (Stebbing, 1883)
Epimeria annabellae Coleman, 1994
Epimeria extensa Andres, 1985
Epimeria georgiana Schellenberg, 1931a
Epimeria grandirostris (Chevreux, 1912a)
Epimeria heldi Coleman, 1998
Epimeria inermis Walker, 1903a
Epimeria intermedia Schellenberg, 1931a
Epimeria macrodonta Walker, 1906b
Epimeria monodon Stephensen, 1947a
Epimeria oxycarinata Coleman, 1990b
Epimeria pulchra Coleman, 1990b
Epimeria puncticulata K.H. Barnard, 1930
Epimeria reoproi Lörz & Coleman, 2001

Epimeria rimicarinata Watling & Holman, 1980
Epimeria robusta K.H. Barnard, 1930
Epimeria rubriques De Broyer & Klages, 1991
Epimeria similis Chevreux, 1912a
Epimeria vaderi Coleman 1998b
Epimeria sp. 1 Andres, 1985
Epimeriella macronyx Walker, 1906b
Epimeriella scabrosa K.H. Barnard, 1930
Epimeriella truncata Andres, 1985
Epimeriella walkeri K.H. Barnard, 1930
Metepimeria acanthurus Schellenberg, 1931a
Parepimeriella irregularis Schellenberg, 1931a
Uschakoviella echinophora Gurjanova, 1955b

IPHIMEDIOIDEA : IPHIMEDIIDAE

[See Coleman & Barnard, 1991b: 261-262.]

Anchiphimedia dorsalis K.H. Barnard, 1930
Echiniphimedia barnardi Coleman & Andres, 1988
Echiniphimedia echinata Walker, 1906c
Echiniphimedia gabriellae Coleman & Andres, 1988
Echiniphimedia hodgsoni Walker, 1906c
Echiniphimedia imparidentata (Bellan-Santini, 1972a)
Echiniphimedia scotti K.H. Barnard, 1930
Echiniphimedia waegelei Coleman & Andres, 1988
Gnathiphimedia barnardi Thurston, 1974b
Gnathiphimedia fuchsi Thurston, 1974a
Gnathiphimedia incerta Bellan-Santini, 1972a
Gnathiphimedia macrops K.H. Barnard, 1932
Gnathiphimedia mandibularis K.H. Barnard, 1930

- Gnathiphimedia sexdentata* (Schellenberg, 1926a)
Gnathiphimedia urodentata Bellan-Santini & Ledoyer, 1987
Gnathiphimedia watlingi Coleman, 1994
Iphimedia imparilabia Watling & Holman, 1980
Iphimedia macrocystidis (K.H. Barnard, 1932)
Iphimedia magellanica Watling & Holman, 1980
Iphimedia multidentata (Schellenberg, 1931a)
Iphimedia pacifica Stebbing, 1883
Iphimedia spinosa (Thomson, 1880a)
Iphimediella acuticoxa Watling & Holman, 1980
Iphimediella bransfieldi K.H. Barnard, 1932
Iphimediella cyclogena K.H. Barnard, 1930
Iphimediella dominici Coleman, 1996
Iphimediella georgei Watling & Holman, 1980
Iphimediella margueritei Chevreux, 1912a
Iphimediella microdentata (Schellenberg, 1926a)
Iphimediella paracuticoxa Andres, 1988
Iphimediella rigida K.H. Barnard, 1930
Iphimediella ruffoi Coleman, 1996
Iphimediella serrata (Schellenberg, 1926a)
Labriphimedia pulchridentata Stebbing, 1883
Labriphimedia vespucii K.H. Barnard, 1931a
Maxilliphimedia longipes (Walker, 1906c)
Nodotergum bicarinatum Bellan-Santini, 1972a
Paranchiphimedia monodi Ruffo, 1949
Parapanoploea longirostris Bellan-Santini, 1972a
Parapanoploea oxygnathia Nicholls, 1938
Parapanoploea recessa Andres, 1988b
Pariphimedia incisa Andres, 1985
Pariphimedia integricauda Chevreux, 1906a

Pariphimedia normani (Cunningham, 1871)

Pseudiphimediella glabra (Schellenberg, 1931a)

Pseudiphimediella nodosa (Dana, 1852a)

Stegopanoploea joubini (Chevreux, 1912a)

IPHIMEDIOIDEA : OCHLESIDAE

[Coleman & Barnard 1991b: 259-260; 262-263; 1991c: 269-270. Berge *et al.*
1999]

Antarctodius antarcticus (Watling & Holman, 1981)

Antarctodius rauscherti Coleman & Kauffeldt, 2001

Curidia magellanica Coleman & Barnard, 1991c

LAPHYSTIOPSIDAE

Prolaphystiopsis platyceras Schellenberg, 1931a

Prolaphystius isopodops K.H. Barnard, 1930

LEPECHINELLIDAE

[re-established by Andres & Brandt, 2001]

Lepechinella cachi J.L. Barnard, 1973a

Lepechinella cetrata K.H. Barnard, 1932

Lepechinella drygalskii Schellenberg, 1926a

Lepechinella huaco J.L. Barnard, 1973b

Lepechinelloides weddellensis Andres & Brandt, 2001

Paralepechinella occultolongicornis Andres & Brandt, 2001

LEUCOTHOIDAE

Leucothoe orkneyi Holman & Watling, 1983

Leucothoe spinicarpa (Abildgaard, 1789) *s.l.*

Leucothoe sp. Branch *et al.*, 1991

LILJEBORGIIDAE

Liljeborgia chevreuxi Stebbing, 1888

Liljeborgia consanguinea Stebbing, 1888

Liljeborgia dubia (Haswell, 1879)

Liljeborgia eurycrada Thurston, 1974b

Liljeborgia georgiana Schellenberg, 1931a

Liljeborgia kerguelenensis Bellan-Santini & Ledoyer, 1974

Liljeborgia georgiensis K.H. Barnard, 1932

Liljeborgia falklandica K.H. Barnard, 1932

Liljeborgia longicornis (Schellenberg, 1931a)

Liljeborgia macrodon Schellenberg, 1931a

Liljeborgia octodentata Schellenberg, 1931a

Liljeborgia proxima Chevreux, 1907a

Liljeborgia pseudomacronyx Bellan-Santini & Ledoyer, 1987

Liljeborgia quadridentata Schellenberg, 1931a

Liljeborgia quinquedentata Schellenberg, 1931a

. LYSIANASSOIDEA

[Family arrangement according to Lowry unpubl. 1998]

LYSIANASSOIDEA : ADELIELLID GROUP

Adeliella laticornis Nicholls, 1938

Adeliella olivieri De Broyer, 1975b

Ambasiopsis georgiensis K.H. Barnard, 1931a

Ambasiopsis tumicornis Nicholls, 1938

Ambasiopsis uncinata K.H. Barnard, 1932

LYSIANASSOIDEA : ALICELLID GROUP

Paralicella similis Birstein & Vinogradov, 1960

LYSIANASSOIDEA : AMARYLLIDID GROUP

Amaryllis macrophthalmus Haswell, 1879a

Erikus dahli Lowry & Stoddart, 1987

LYSIANASSOIDEA : ARISTIIDAE

Aristias antarcticus Walker, 1906a

Aristias collinus K.H. Barnard, 1932

LYSIANASSOIDEA : CYPHOCARIDIDAE

Cyphocaris anonyx Boeck, 1871b

Cyphocaris challengerii Stebbing, 1888

Cyphocaris faurei K.H. Barnard, 1916

Cyphocaris richardi Chevreux, 1905e

LYSIANASSOIDEA : EURYTHENEID GROUP

Eurythenes gryllus (Lichtenstein, 1822)

Eurythenes obesus (Chevreux, 1905a)

LYSIANASSOIDEA : HIRONDELLEID GROUP

Hirondellea antarctica (Schellenberg, 1926a)

LYSIANASSOIDEA : KERGUELENEID GROUP

Kerguelenia adeliensis Bellan-Santini, 1972a

Kerguelenia antarctica K.H. Barnard, 1930

Kerguelenia antiborealis Bellan-Santini & Ledoyer, 1987

Kerguelenia compacta Stebbing, 1888

Kerguelenia glacialis Schellenberg, 1926a

? *Kerguelenia palpalis* K.H. Barnard, 1932

LYSIANASSOIDEA : LEPIDEPECREELID GROUP

Lepidepecreella ctenophora Schellenberg, 1926a

Lepidepecreella emarginata Nicholls, 1938

Lepidepecreella ovalis K.H. Barnard, 1932

Lepidepecreella tridactyla Bellan-Santini, 1972a

LYSIANASSOIDEA : LYSIANASSIDAE S.S.

[see Lowry & Stoddart 1997]

Lysianassinae

- Acontiosoma marionis* Stebbing, 1888
Aruga falklandica (K.H. Barnard, 1932)
Kakanui integricauda (Stebbing, 1888)
Kakanui punui Lowry & Stoddart, 1983b
Lysianopsis subantarctica (Schellenberg, 1931a)
Lysianopsis tieke Lowry & Stoddart, 1983b
Parambasia rossii Stephensen, 1927e
Parawaldeckia hirsute Lowry & Stoddart, 1983b
Parawaldeckia kidderi (Smith, 1876)
Parawaldeckia suzae Lowry & Stoddart, 1983b
Parawaldeckia vesca Lowry & Stoddart, 1983b
Parawaldeckia sp. 1 J.L. Barnard, 1972b
Parawaldeckia sp. 2 Stephensen, 1949
Socarnoides kergueleni Stebbing, 1888

Socarnoides unidentatus (Schellenberg, 1931a)
Stomacontion acutibasalis (Bellan-Santini & Ledoyer, 1974)
Stomacontion bulbus Rauschert, 1997a
Stomacontion hurleyi Lowry & Stoddart, 1983b
Stomacontion insigne K.H. Barnard, 1932
Stomacontion pepinii (Stebbing, 1888)
Stomacontion pungapunga Lowry & Stoddart, 1983b
Waldeckia arnaudi (Bellan-Santini, 1972a)
Waldeckia chevreuxi Stebbing, 1910a
Waldeckia obesa (Chevreux, 1905d)
Waldeckia sp. Takeuchi et al. 2001

Tryphosinae

- Allogaussia galeata* Schellenberg, 1926a
 ? *Allogaussia navicula* (K.H. Barnard, 1932)
Allogaussia paradoxa (Schellenberg, 1926a)
Cheirimedon crenatipalmatus Stebbing, 1888
Cheirimedon femoratus (Pfeffer, 1888)
Cheirimedon fougneri Walker, 1903a

Cheirimedon similis Thurston, 1974b
Cheirimedon solidus Andres, 1986

Falklandia reducta (Schellenberg, 1931a)
Hippomedon incisus K.H. Barnard, 1930

Hippomedon kergueleni (Miers, 1875a)
Hippomedon macrocephalus Bellan-Santini, 1972a
Hippomedon major (K.H. Barnard, 1932)
Lepidepecreoides xenopus K.H. Barnard, 1931a
Lepidepecreum cingulatum K.H. Barnard, 1932
Lepidepecreum foraminiferum Stebbing, 1888

Lepidepecreum infissum Andres, 1983
Lepidepecreum urometacarinatum Andres, 1985
Lysianella morbihanensis (Bellan-Santini & Ledoyer, 1974)
 ? *Orchomene* sp. Takeuchi et al. 2001
 ? *Orchomenella* (*Orchomenella*) *chelipes* (Walker, 1906a)
Orchomenella (*Orchomenella*) *franklini* (Walker, 1903a)
Orchomenella (*Orchomenella*) *guillei* De Broyer, 1985a
Orchomenella (*Orchomenella*) *hureaui* (De Broyer, 1973)
Orchomenella (*Orchomenella*) *kryptopinguides* (Andres, 1983)
Orchomenella (*Orchomenella*) *pinguides* (Walker, 1903a)

Orchomenella (Orchomenella) ultima (Bellan-Santini, 1972b)
Orchomenella (Orchomenopsis) aahu (Lowry & Stoddart, 1983b)
Orchomenella (Orchomenopsis) acanthura (Schellenberg, 1931a)
Orchomenella (Orchomenopsis) cavimanus (Stebbing, 1888)
Orchomenella (Orchomenopsis) cavimana rostrata (Schellenberg, 1931a)
Orchomenella (Orchomenopsis) chilensis (Heller, 1868)
Orchomenella (Orchomenopsis) denticulata Rauschert, 1995
Orchomenella (?Orchomenopsis) goniops (Walker, 1906a)
Orchomenella (?Orchomenopsis) hiata (Andres, 1983)
Orchomenella (?Orchomenopsis) macrophthalma (Birstein & Vinogradov, 1962b)

Orchomenella (Orchomenopsis) rotundifrons (K.H. Barnard, 1932)
Orchomenella (Orchomenopsis) zschaui (Pfeffer, 1888)
Orchomenyx macronyx (Chevreux, 1905d)
Orchomenyx schellenbergi (Thurston, 1972)
Orchomenyx tabarini (Thurston, 1972)
Paralysianopsis odhneri Schellenberg, 1931a
Pseudokoroga barnardi Schellenberg, 1931a
Pseudorchomene coatsi (Chilton, 1912a)
Stephensenia haematopus Schellenberg, 1928a
Tryphosella analogica (K.H. Barnard, 1932)
Tryphosella bispinosa (Schellenberg, 1931a)
Tryphosella castellata (K.H. Barnard, 1932)
Tryphosella cicadopsis (Schellenberg, 1926a)
Tryphosella intermedia (Schellenberg, 1926a)
Tryphosella longitelson (K.H. Barnard, 1932)
Tryphosella macropareia (Schellenberg, 1926a)
Tryphosella marri Thurston, 1974b
Tryphosella murrayi (Walker, 1903a)
?Tryphosella paramoi (Schellenberg, 1931a)

Tryphosella schellenbergi Lowry & Bullock, 1976
Tryphosella serans Lowry & Stoddart, 1983b
?Tryphosella serrata (Schellenberg, 1931a)
Tryphosella triangularis (K.H. Barnard, 1932)
Tryphosella trigonica (Stebbing, 1888)
Tryphosites chevreuxi Stebbing, 1914b
Tryphosites sp. Andres, 1975b
Tryphosoides falcata Schellenberg, 1931a

Uristinae

Abyssorchomene charcoti (Chevreux, 1912a)
Abyssorchomene nodimanus (Walker, 1903a)
Abyssorchomene plebs (Hurley, 1965a)
Abyssorchomene rossi (Walker, 1903a)
Abyssorchomene scotianensis (Andres, 1983)
Cicadosa cicadoides (Stebbing, 1888)
Parschisturella carinata (Schellenberg, 1926a)
Parschisturella simplex Andres, 1983
Pseudonesimoides cornutilabris Bellan-Santini & Ledoyer, 1974
Uristes adarei (Walker, 1903a)
Uristes albinus (K.H. Barnard, 1932)
Uristes barbatipes Stebbing, 1888)
Uristes georgianus (Schellenberg, 1931a)
Uristes gigas Dana, 1849
Uristes mediator J.L. Barnard, 1962d

Uristes serratus Schellenberg, 1931a
Uristes stebbingi (Walker, 1903a)
Uristes subchelatus (Schellenberg, 1931a)

LYSIANASSOIDEA : OPISIDAE

Podoprionides incerta Walker, 1906a

LYSIANASSOIDEA : PACHYNID GROUP

Acidostomatine Group

Shackletonia robusta K.H. Barnard, 1931a

Pachynine Group

Drummondia sculptidentata Ren, 1991

Ekelofia oculata (Schellenberg, 1931a)

Figorella macrophocolata Ren, 1991

Figorella tanidea J.L. Barnard, 1962d

Pachychelium antarcticum Schellenberg, 1926a

Pachychelium barnardi Alonso de Pina, 1993

Pachychelium nichollsi Lowry, 1984b

Pachychelium schellenbergi Lowry, 1984b

Sophrosynine Group

Sophrosyne antarctica Ren, 1991

Sophrosyne murrayi Stebbing, 1888

LYSIANASSOIDEA : SCOPELOCHEIRIDAE

Paracallisoma alberti Chevreux, 1903

Scopelocheiropsis abyssalis Schellenberg, 1926a

Scopelocheirus schellenbergi Birstein & Vinogradov, 1958

LYSIANASSOIDEA : THORIELLID GROUP

Chevreuxiella obensis Birstein & Vinogradov, 1962b

Danaella mimonectes Stephensen, 1925b

LYSIANASSOIDEA : INCERTAE SEDIS

[fide BK91]

Gainella chelata Chevreux, 1912a

Stenia magellanica Dana, 1852a

MELPHIDIPPIDAE

[see Barnard & Barnard 1983: 607]

Melphidippa antarctica Schellenberg, 1926a

Melphidippa serrata (Stebbing, 1888)

Melphisubchela prehenda Andres, 1981b

OEDICEROTIDAE

Carolobatea schneideri (Stebbing, 1888)

Carolobatea sp. J.L. Barnard, 1972b

Halicreion vanhoeffeni Schellenberg, 1926a
Monoculodes antarcticus K.H. Barnard, 1932
Monoculodes jazdzewskii De Broyer, 1980
Monoculodes scabriculosus K.H. Barnard, 1932
Monoculopsis vallentini Stebbing, 1914b
Oediceroides calmani Walker, 1906b
Oediceroides cinderella Stebbing, 1888
Oediceroides emarginatus Nicholls, 1938
Oediceroides lahillei lahillei Chevreux, 1911b
Oediceroides lahillei polita Schellenberg, 1931a
Oediceroides macrodactylus Schellenberg, 1931a
Oediceroides newnesi (Walker, 1903a)
Oediceroides rostratus (Stebbing, 1883)
Oediceroides similis Nicholls, 1938
Paramonoculopsis acuta Alonso de Pina, 1997
?Paraperiiculodes belgicae Ruffo, 1949
Paraperiiculodes brevimanus K.H. Barnard, 1931a
Paraperiiculodes brevirostris (Schellenberg, 1931a)
Paraperiiculodes cystiferus (Schellenberg, 1931a)
Paraperiiculodes microrhynchus Ruffo, 1949
Paroediceroides sinuatus Schellenberg, 1931a

PAGETINIDAE

Pagetina antarctica Andres, 1981
Pagetina genarum K.H. Barnard, 1931a
Pagetina monodi (Nicholls, 1938)
Pagetina reducta Holman & Watling, 1981

PARDALISCIDAE

- Halice macronyx* (Stebbing, 1888)
Halice profundus K.H. Barnard, 1932
Halice secunda (Stebbing, 1888)
Halice tenella Birstein & Vinogradov, 1962b
Halicella parasitica Schellenberg, 1926a
Necochea pardella J.L. Barnard, 1962d
Nicippe unidentata K.H. Barnard, 1932
Pardalisca abyssoides K.H. Barnard, 1932
Pardalisca magellanica Schellenberg, 1931a
Pardalisca marionis Stebbing, 1888

PHLIANTIDAE

- Iphinotus typicus* (Thomson, 1882)

PHOXOCEPHALIDAE

[check Bnd & Drummond 1978]

- Cephalophoxoides kergueleni* (Stebbing, 1888)
Coxophoxus coxalis (K.H. Barnard, 1932)
Fuegiphoxus abjectus Barnard & Barnard, 1980
Fuegiphoxus fuegiensis (Schellenberg, 1931a)
Fuegiphoxus inutilis Barnard & Barnard, 1980
Fuegiphoxus uncinatus (Chevreux, 1912a)
Harpiniopsis aciculum Ren, 1991
Harpiniopsis wandichia (J.L. Barnard, 1962d)
Heterophoxus pellusidus Ren, 1991
Heterophoxus trichosus K.H. Barnard, 1932

Heterophoxus videns K.H. Barnard, 1930
Leptophoxoides molaris J.L. Barnard, 1962d
Metharpinia longirostris Schellenberg, 1931a
Metharpinia protuberantis Alonso de Pina, 2001.
Microphoxus cornutus (Schellenberg, 1931a)
Palabriaphoxus latifrons (Ren, 1991)
Parafoxiphalus longicarpus Alonso de Pina, 2001.
?Paraphoxus latipes Ren, 1991
?Paraphoxus pyripes K.H. Barnard, 1930
?Parharpinia obliqua K.H. Barnard, 1932
?Parharpinia rotundifrons K.H. Barnard, 1932
Phoxorgia sinuata (K.H. Barnard, 1932)
Proharpinia antipoda Schellenberg, 1931a
Proharpinia stephensi (Schellenberg, 1931a)
Pseudfoxiphalus setosus Andres, 1991
Pseudharpinia antarctica Ren, 1991
Pseudharpinia calcariaria Bushueva, 1982
Pseudharpinia cariniceps (K.H. Barnard, 1932)
Pseudharpinia dentate Schellenberg, 1931a
Pseudharpinia obtusifrons (Stebbing, 1888)
Pseudharpinia vallini (Dahl, 1954)
Torridoharpinia hurleyi (J.L. Barnard, 1958a)

PHOXOCEPHALOPSIDAE

Eophoxocephalopsis colombus Alonso de Pina, 2000.
Eophoxocephalopsis deceptionis (Stephensen, 1947a).
Eophoxocephalopsis rhachianensis Thurston, 1989a
Phoxocephalopsis gallardoi Barnard & Clark, 1984
Phoxocephalopsis zimmeri Schellenberg, 1931a

Puelche orensanzi Barnard & Clark, 1982a

PLATYISCHNOPIDAE

Eudevenopus gracilipes (Schellenberg, 1931a)

PLEUSTIDAE

Austropleustes cuspidatus K.H. Barnard, 1931a

?*Austropleustes simplex* K.H. Barnard, 1932

Mesopleustes abyssorum (Stebbing, 1888)

Parepimeria bidentata Schellenberg, 1931a

Parepimeria crenulata Chevreux, 1912a

Parepimeria irregularis (Schellenberg, 1931a)

Parepimeria major K.H. Barnard, 1932

Parepimeria minor Watling & Holman, 1980

?*Pleusymtes* sp. 1. Branch *et al.*, 1991

PONTOPOREIIDAE

[see Bnd & Bnd, 1983: 562]

Zaramilla kergueleni Stebbing, 1888

PSEUDAMPHILOCHIDAE

Pseudamphilochus shoemakeri Schellenberg, 1931a

SEBIDAE

- Seba antarctica* Walker, 1906c
?Seba georgiana Schellenberg, 1931a
Seba saundersii Stebbing, 1875b
Seba stoningtonensis Thurston, 1974b
Seba subantarctica Schellenberg, 1931a
Seba typical (Chilton, 1884a)
Seba sp. 1 Holman & Watling, 1983b
Seba sp.2 Holman & Watling, 1983b

STEGOCEPHALIDAE

[see Berge, De Broyer & Vader, 2000; Berge & Vader 2001]

Andaniexinae

- Andaniexis ollii* Berge, De Broyer & Vader, 2000
Andaniotes abyssorum Stebbing, 1888.
Andaniotes linearis K.H. Barnard, 1932
Andaniotes pooh Berge 2001b
Andaniotes pseudolinearis Berge 2001b
Parandaniexis dewitti Watling & Holman, 1980
Stegosoladidus antarcticus Berge, 2001a
Stegosoladidus debroyeri Berge, 2001a
Stegosoladidus ingens (Chevreux, 1906e)

Andaniopsinae

Andaniopsis integripes (Bellan-Santini & Ledoyer, 1987)

Parandaniinae

Parandania boeckii (Stebbing, 1888)

Parandania gigantea (Stebbing, 1883)

Parandania nonhiata Andres, 1985

Stegocephalinae

Austrophippisia unihamata (Berge & Vader, 2000)

Schellenbergia vanhoeffeni (Schellenberg, 1926a)

Stegocephalus kergueleni (Schellenberg, 1926a)

Stegocephalus rostrata K.H. Barnard, 1932

Stegomorphia watlingi (Berge, De Broyer & Vader, 2000).

Stegocephalina pacis (Bellan-Santini & Ledoyer, 1974)

Tetradeion crassum (Chilton, 1883)

STENOTHOIDAE

Antatelson antennatum Bellan-Santini & Ledoyer, 1974

Antatelson cultricauda (K.H. Barnard, 1932)

Antatelson rostratum Bellan-Santini & Ledoyer, 1974

Antatelson tuberculatum Andres, 1989

Antatelson walkeri (Chilton, 1912a)

Aurometopa aurorae (Nicholls, 1938)

Mesoproboloides cornuta (Schellenberg, 1926a)

Mesoproboloides similis (Schellenberg, 1926a)

Mesoproboloides spinosa Bellan-Santini & Ledoyer, 1974
Metopoides antarcticus (Walker, 1906b)
Metopoides clavata Schellenberg, 1931a
Metopoides crassa Schellenberg, 1931a
Metopoides curvipes Schellenberg, 1926a
Metopoides elliptica Schellenberg, 1931a
Metopoides heterostylis Schellenberg, 1926a
Metopoides lanceolatus Rauschert, 1990a
Metopoides latus Rauschert, 1990a
Metopoides leptomanus Rauschert, 1990a
Metopoides longicornis Schellenberg, 1931a
Metopoides macrocheir Schellenberg, 1926a
Metopoides magellanica (Stebbing, 1888)
Metopoides sarsi (Pfeffer, 1888)
Metopoides sp.1 Bellan-Santini & Ledoyer, 1974
Metopoides sp.2 Jazdzewski *et al.*, 1992
Metopoides typicaminus Andres, 1995
Paraprobolisca leptopoda Ren, 1991
Parathaumatelson nasicum (Stephensen, 1927e)
Probolisca elliptica (Schellenberg, 1931a)
Probolisca nasutigenes (Stebbing, 1888)
Probolisca ovata (Stebbing, 1888)
Proboloides typica (Walker, 1906b)
Proboloides sp.1 Stephensen, 1947a [
Proboloides sp.2 Branch *et al.*
Proboloides sp.3 Branch *et al.*
Prometopa dorsoundata Bushueva, 1988
Prometopa edentata Rauschert, 1990a
? *Prometopa longipalma* Ren, 1991
Prometopa tuberculata Schellenberg, 1926a

- Prothaumatelson nasutum* (Chevreux, 1912a)
Pseudothaumatelson cyproides Nicholls, 1938
Pseudothaumatelson patagonicum Schellenberg, 1931a
Scaphodactylus bentarti Rauschert, 1995
Scaphodactylus foliodactylus (Rauschert, 1990a).
Scaphodactylus gigantocheirus Rauschert & Andres, 1993.
Scaphodactylus simus Rauschert & Andres, 1994
Scaphodactylus sp. 1 Rauschert & Andres, 1993.
Scaphodactylus sp. 2 Rauschert & Andres, 1993.
Scaphodactylus sp. 3 Rauschert & Andres, 1993.
Stenothoe aucklandicus Stephensen, 1927e
Stenothoe falklandica Schellenberg, 1931a
Stenothoe magellanica Rauschert, 1998
Stenothoe sivertseni Stephensen, 1949
Stenothoe sp.1 Bellan-Santini & Ledoyer, 1987
Thaumatelson herdmani Walker, 1906b
Thaumatelsonella kingelepha Rauschert & Andres, 1991
Torometopa andresi (Rauschert, 1990a)
Torometopa angustus Rauschert, 1990a
Torometopa antarctica (Walker, 1906b)
?Torometopa bellansantini (Bushueva, 1988)
Torometopa carinata (Schellenberg, 1931a)
Torometopa compacta (Stebbing, 1888)
Torometopa crassicornis (Schellenberg, 1931a)
Torometopa crenatipalmata (Stebbing, 1888)
Torometopa crypta Andres & Rauschert, 1992.
Torometopa dentimanus (Nicholls, 1938)
Torometopa elephantensis Andres & Rauschert, 1992.
?Torometopa laevis (Ren, 1991)
Torometopa macromanus (Rauschert, 1990a)

Torometopa nitita (Ren, 1991)

Torometopa palmata (Ruffo, 1949)

Type specimen location:

Torometopa parallelocheir (Stebbing, 1888)

Torometopa perlata (K.H. Barnard, 1930)

Torometopa porcellana (K.H. Barnard, 1932)

Torometopa pseudoperlata Andres, 1993.

Torometopa serrata (Rauschert, 1990a)

Torometopa stephensi (Ruffo, 1949)

Torometopa sp.1 Andres & Rauschert, 1992.

Torometopa sp.2 Andres, 1993.

STILIPEDIDAE

Alexandrella australis (Chilton, 1912a)

Alexandrella dentata Chevreux, 1912a

Alexandrella inermis Bellan-Santini & Ledoyer, 1987

Alexandrella mixta (Nicholls, 1938)

Alexandrella pulchra Ren, 1991

Bathypanoploea schellenbergi Holman & Watling, 1983a

SYNOPIIDAE

Bruzelia poton J.L. Barnard, 1972c

Cardenio paurodactylus Stebbing, 1888

Syrrhoe nodulosa K.H. Barnard, 1932

Syrrhoe psychrophila Monod, 1926

Syrrhoe tuberculata Dahl, 1954

Syrrhoites anaticauda K.H. Barnard, 1930

Syrrhoites sorpresa (J.L. Barnard, 1962d)

Tiron antarcticus K.H. Barnard, 1932

TALITRIDAE

Allorchestes compressa Dana, 1852a

Allorchestes novizealandiae Dana, 1852a

Allorchestes sp.1 Stephensen, 1938c

Platorchestia platensis (Kroyer 1845)

? *Orchestia scutigerula* Dana, 1853

Orchestoidea tuberculata Nicolet, 1849

Protorchestia nitida (Dana, 1852a)

Transorchestia chiliensis (Milne-Edwards, 1840)

UROHAUSTORIIDAE

Huarpe escofeti Barnard & Clark, 1982b

UROTHOIDAE

Carangolia cornuta Bellan-Santini & Ledoyer, 1987

Urothoe falcata Schellenberg, 1931a

?*Urothoe latifrons* Ren, 1991

Urothoe marionis Bellan-Santini & Ledoyer, 1987

Urothoe oniscoides (K.H. Barnard, 1932)

Urothoe vema J.L. Barnard, 1962d

Urothoides lachneessa (Stebbing, 1888)

VALETTIIDAE

Valettia coheres Stebbing, 1888

ZOBACHOIDAE

Chono angustiarum Clark & Barnard, 1987

Tonocote introflexidus Clark & Barnard, 1988

Tonocote magellani Clark & Barnard, 1986

II. SOUS-ORDRE COROPHIIDEA

Leach, 1814

INFRAORDER COROPHIIDA Leach, 1814

Superfamily AOROIDEA Stebbing, 1899c

FAMILY AORIDAE STEBBING, 1899C

Aora anomala Schellenberg, 1926a

Aora kergueleni Stebbing, 1888

Aora maculata (Thomson, 1879b)

Aora trichobostrycha Stebbing, 1888

Aora typica Kroyer, 1845

Aora sp. 1 Nicholls, 1938

Bemlos kergueleni (Stebbing, 1888)

Lembos argentinensis Alonso de Pina, 1992

Lembos fuegiensis Dana, 1853 [AV genus]

Lembos sp. 1 J.L. Barnard, 1972b

Lembos sp. 2 J.L. Barnard, 1972b = *Meridiolembos pertinax* Myers, 1981c

Lembos sp. 3 J.L. Barnard, 1972b

Lembos sp. 4 Bellan-Santini & Ledoyer, 1987

Meridiolembos acherontis Myers, 1981c

Meridiolembos pertinax Myers, 1981c

Microdeutopus sp. 1 Stephensen, 1927e

Superfamily Corophioidea Leach, 1814

FAMILY AMPITHOIDAE BOECK, 1871

Subfamily Ampithoinae Boeck, 1871

Ampithoe kergueleni Stebbing, 1888

Ampithoe valida Smith, 1873

Peramphithoe femorata (Kroyer, 1845)

FAMILY COROPHIIDAE Leach, 1814

Subfamily Corophiinae Leach, 1814

Corophinae: Tribe Corophiini, Leach, 1814

Crassikorophium bonellii (Milne Edwards, 1830)

Corophium cylindricum (Say, 1818)

Corophinae: Tribe Haplocheirini Myers & Lowry, 2003

Anonychocheirus richardsoni Moore & Myers, 1983

Haplocheira balssi Schellenberg, 1931a

Haplocheira barbimana (Thomson, 1879b)

Haplocheira barbimana barbimana (Thomson, 1879b)
Haplocheira barbimana robusta K.H. Barnard, 1932
Haplocheira barbimana typica Haswell, 1879a
Haplocheira plumosa Stebbing, 1888
Kuphocheira emancipata Moore & Myers, 1983
Kuphocheira setimana K.H. Barnard, 1931a

Infraorder CAPRELLIDA Leach, 1814

Superfamily CAPRELLOIDEA LEACH, 1814

FAMILY CAPRELLIDAE LEACH, 1814

Subfamily Caprellinae Leach, 1814

Caprella equilibra Say, 1818
Caprella manneringi McCain, 1979
Caprella penantis Leach, 1814
Caprella unguina Mayer, 1903
Caprella sp. McCain & Gray, 1971
Caprellaporema subantarctica Guerra-García 2003a
Deutella vema (McCain & Gray, 1971)
?Eupariambus sp. Branch *et al.*, 1991
Mayerella magellanica McCain & Gray, 1971
Protella trilobata McCain & Gray, 1971
Protellopsis kergueleni Stebbing, 1888
Pseudaeginella campbellensis Guerra-García, 2003a
Pseudaeginella tristanensis Stebbing, 1888
Triantella solitaria Mayer, 1903

Subfamily Phtisicinae Vassilenko, 1968

- Aeginoides gaussi* Schellenberg, 1926b
Caprellina longicollis (Nicolet, 1849)
? *Caprellina longicollis* (Nicolet, 1849)
Caprellinoides antarcticus Schellenberg, 1926(to be revised)
Caprellinoides mayeri (Pfeffer, 1888)
Caprellinoides mayeri Barnard, 1930 (to be revised)
Caprellinoides singularis Guerra-García, 2001c
Caprellinoides spinosus (Pfeffer, 1888) (to be revised)
Caprellinoides tristanensis Stebbing, 1888
Caprellinoides tristanensis Stebbing, 1888 (to be revised)
Dodecas elongata Stebbing, 1883
Dodecasella elegans K.H. Barnard, 1931
Dodecasella georgiana (Schellenberg, 1931a)
Paraproto sp.
Pseudododecas bowmani McCain & Gray, 1971
Pseudoprotomima hedgpethi McCain & Gray, 1971

FAMILY CYAMIDAE RAFINESQUE, 1815

- Cyamus balaenopterae* K.H. Barnard, 1931
Cyamus boopis Lütken, 1870
Cyamus catodontis Margolis, 1954
Cyamus erraticus Roussel de Vauzème, 1834
Cyamus gracilis Roussel de Vauzème, 1834
Cyamus ovalis Roussel de Vauzème, 1834
Isocyamus antarcticensis Vlasova in Berzin & Vlasova, 1982

CAPRELLOIDEA: FAMILY DULICHIIDAE DANA, 1849

Dulichia antarctica Rauschert, 1988.

Paradyopedos antarcticus Andres & Rauschert, 1990

Pseudodulichia antarctica (Rauschert, 1988)

CAPRELLOIDEA: FAMILY PODOCERIDAE LEACH, 1814

Neoxenodice caprellinoides Schellenberg, 1926b

Neoxenodice cryophile Lowry, 1976

Neoxenodice hoshiai Takeuchi & Takeda, 1992

Podocerus brasiliensis (Dana, 1853)

Podocerus capillimanus Nicholls, 1938

Podocerus cristatus rotundatus Schellenberg, 1931a

Podocerus danae (Stebbing, 1888)

Podocerus danae armatus Bellan-Santini & Ledoyer, 1987

Podocerus ornatus (Miers, 1875a)

Podocerus septemcarinatus Schellenberg, 1926a

Podocerus sp. 1. K.H. Barnard, 1932

SUPERFAMILY PHOTOIDEA Boeck, 1871

PHOTOIDEA: Family ISChyroceridae STEBBING, 1899C

Subfamily Ischyrocerinae Stebbing, 1899c

Tribe Ischyrocerini Stebbing, 1899c

Ischyrocerus camptonyx Thurston, 1974a
Ischyrocerus hortator J.L. Barnard, 1964d
Ischyrocerus longimanus (Haswell, 1879b)
?Ischyrocerus sp.1 Bellan-Santini & Ledoyer, 1987
?Ischyrocerus sp.2 Branch *et al.*, 1991
Jassa alonsoae Conlan, 1990
Jassa falcata Montagu, 1808 s.l.
Jassa fenwicki Conlan, 1990
?Jassa goniamera Walker, 1903a
Jassa ingens Pfeffer, 1888
Jassa justii Conlan, 1990
?Jassa multidentata Schellenberg, 1931a
Jassa thurstoni Conlan, 1990
?Jassa wandeli Chevreux, 1906e
Jassa sp. 1 Stephensen, 1927e
Jassa sp. 2 Stephensen, 1947a
Parajassa tristanensis (Stebbing, 1888)
Pseudischyrocerus crenatipes Bellan-Santini & Ledoyer, 1987
Pseudischyrocerus denticauda Schellenberg, 1931a
Pseudischyrocerus distichon (K.H. Barnard, 1930)
Ventojassa georgiana (Schellenberg, 1931a)

Ischyrocerinae: Tribe Siphonoecetini Just, 1983

Cerapus oppositus K.H. Barnard, 1932
Cerapus sismithi Stebbing, 1888
Pseuderichthonius gaussi Schellenberg, 1926a
Pseuderichthonius hesperidesi Rauschert, 1997
Pseuderichthonius inflatus Ren, 1991

PHOTOIDEA: FAMILY PHOTIDAE BOECK, 1871

- Gammaropsis* (*Gammaropsis*) *bennetti* Thurston, 1974b
Gammaropsis (*Gammaropsis*) *ctenura* (Schellenberg, 1931a)
Gammaropsis (*Gammaropsis*) *deseadensis* Alonso, 1981
Gammaropsis (*Gammaropsis*) *exsertipes* Stebbing, 1888
Gammaropsis (*Gammaropsis*) *georgiana* (Schellenberg, 1931a)
Gammaropsis (*Gammaropsis*) *kergueleni* (Schellenberg, 1926a)
Gammaropsis (*Gammaropsis*) *longicornis* Walker, 1906c
Gammaropsis (*Gammaropsis*) *longitarsus* (Schellenberg, 1931a)
Gammaropsis (*Gammaropsis*) *monodi* (Schellenberg, 1931a)
Gammaropsis (*Gammaropsis*) *purpurescens* (K.H. Barnard, 1932)
Gammaropsis (*Gammaropsis*) *remipes* (K.H. Barnard, 1932)
Gammaropsis (*Gammaropsis*) *serricra* (K.H. Barnard, 1932)
Gammaropsis (*Gammaropsis*) *triodon* (Schellenberg, 1926a)
Gammaropsis (*Gammaropsis*) *valdiviae* (Schellenberg, 1926c)
Megamphopus angustilobatus Ren, 1991
Megamphopus dimorpha (K.H. Barnard, 1932)
Megamphopus elephantis K.H. Barnard, 1932
Gammaropsis (*Paranaenia*) *dentifera* (Haswell, 1879b)
Gammaropsis (*Paranaenia*) *typica* (Chilton, 1884a)
Gammaropsis (*Pseudeurystheus*) *sublitoralis* (Schellenberg, 1931a)
Gammaropsis (*Segamphopus*) *blaisus* (K.H. Barnard, 1932)
Gammaropsis sp. 1 Stephensen, 1927e
Gammaropsis sp. 2 Stephensen, 1947a
Gammaropsis sp. 3 Truchot, 1974
Gammaropsis sp. 4 Truchot, 1974
Gammaropsis sp. 5 Branch *et al.*, 1991
Paragammaropsis prenes Ren, 1991

Photis coeca J.L. Barnard, 1962d

Photis macrocarpa Stebbing, 1888

Photis sp. 1 Truchot, 1974

